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MEDICAL ENTOMOLOGY

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CORNELL UNIVERSITY

SECOND
EDITION

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Preface

MORE than seventeen years have passed since the first edition of *Medical Entomology* was published. In the original preface the important role played by insects and other arthropods in the transmission, causation, and spread of human and animal diseases was stressed. Today no such emphasis is needed, for the important role of insects in human welfare was fully demonstrated during World War II. Recognition of the effects of insect-borne diseases on the armies and navies of the belligerents has impelled our medical and entomological services and the governments of all nations to conduct extensive investigations on all phases of the problem. The results of many of these investigations, some of which are continuing, have not yet been published. In the present work the writer has attempted, with varying success, to bring together all data available by the end of 1948.

s completely rewritten text is offered to the physician, the entomologist, the public health worker, the student, and the layman in order to give them an authoritative survey of our present knowledge. The writer has not attempted to usurp the function of the physician, so the reader need not expect to find a discussion of treatment; he will find, however, a brief account of the best known methods of controlling the insects involved in disease transmission or causation. Here great advances have been made during the past few years. The reader is warned, however, that all the newer insecticides must be used with care and directions should be followed carefully.

The literature on insect-borne diseases is voluminous, widely scattered in many and varied journals, monographs, government publications, and other sources, and difficult to cover adequately. For this reason a list of journals, textbooks, and other publications that will enable the student to find the latest information is given at the end of the first chapter of the present work. Furthermore, each chapter is provided with a selected bibliography. Many of the references given have long bibliographies; these references are starred.

The writer gratefully acknowledges his indebtedness to the numerous authors whose publications he has consulted or quoted. Wherever illust material is borrowed, full acknowledgment is given; if, by accident does not appear, due apology is hereby offered. To the many colle friends, and students who have given suggestions, furnished material, a other ways co-operated with him, the writer desires to tender his s thanks. He is under special obligation to Mr. Harvey I. Scudder for the galley proof, and to Mr. C. Y. Chow for checking the manuscri reference to malaria in China.

ROBERT MATHE

Ithaca, New York
September 1949

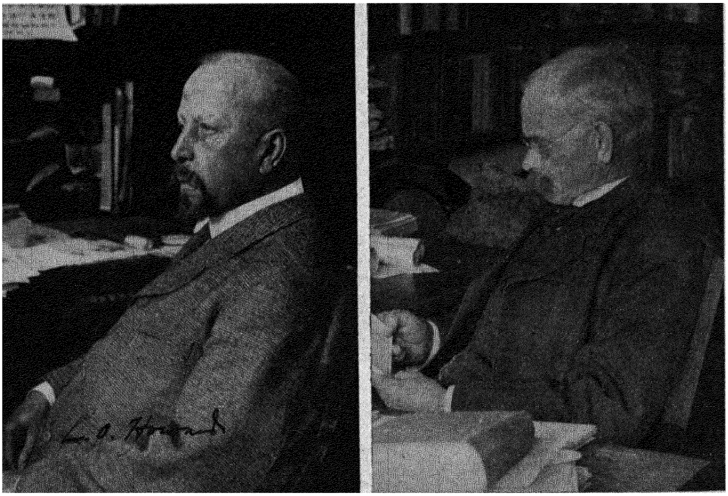

Plate IV. Left: Dr. Leland Ossian Howard (1857–   ), who for nearly thirty-five years served as Chief of the Bureau of Entomology, United States Department of Agriculture, and who did more than any other American to establish the importance of insects as agents in the causation and spread of human disease. *Right:* Professor John Henry Comstock (1849–1931) in his old office in White Hall, Cornell University. By his work and teaching he gave entomology its present position in American universities.

CHAPTER I

Arthropods and Human Disease

THE phylum Arthropoda plays a role in human welfare that is little understood by the great majority of people. In the sea the dominant animal life is not the larger fishes, mammals, etc., but those tiny animals that constitute the greater part of the plankton—the free-swimming, minute Crustacea on which the others rely for food. As free-living vegetarians and scavengers they people the sea in vast numbers and perform their duties with admirable fitness, keeping great bodies of water cleaned of the dead and dying. On the land insects play a similar but more dominant role. For sheer vastness of numbers and incomparable adaptation for meeting the vicissitudes of life they far outrank any other animal or plant association. Who can count the ants that populate our fields and hillsides or the plant lice that suck their nourishment from our wild and cultivated plants? The part insects play in agriculture and commerce has been admirably portrayed by a number of writers and, at times, overemphasized, especially with respect to the vast losses agriculture suffers at their hands. It is not our purpose to enter such a discussion here; the reader will find references at the end of this chapter that will enlighten him on this phase of insect activity. Sufficient for our purposes is the self-evident fact that arthropods, and especially the class Hexapoda (insects), affect human welfare at every point and at times endanger man's very existence or hold in check his advances in the development of some of the most fertile regions of the globe. Medical entomology and parasitology have been recognized as important fields of study and research, not only for the zoologist, but for the physician, the veterinarian, and the layman. World War II amply demonstrated the great need for more knowledge of these subjects.

No more striking and dramatic story could be told than that of the remarkable interrelations which arthropods play in the spread and maintenance of plant, animal, and human diseases. Insects, long regarded and still regarded as unworthy of serious consideration by many of our scientists, have gradually forced peoples and governments to devote some of their resources to studies too long delayed. Here only a bare outline of these studies can be offered and a tribute paid to those great medical leaders and others who have laid down their lives in the investigations of insect-borne diseases.

There are numerous early references to insects as distributors of disease—references made long before the parasitic origin of disease was established. To Mercurialis (1530–1607), an Italian physician, is usually attributed the first concrete observation that flies serve, in some unknown manner, to spread disease. During the plague (Black Death), which ravaged Europe in his day, he observed that flies may spread the disease by feeding on the internal secretions of the dead and dying and then depositing their feces on the food of the well. França states that Souza (1587) suspected flies of spreading yaws (framboesia); Bancroft (1769) propounded a similar theory from his observations in Guiana; and many years later Castellani (1907) demonstrated that flies do play a part in the dissemination of this disease—obtaining the organism (*Treponema pertenue*) from the sores of the sick and passing it on to the well.

It was not till many years later that well-defined theories of insect propagation of disease were promulgated. Such are those of Beauperthuy (1854) and Nott (1848) relative to the carriage of yellow fever by mosquitoes. Beauperthuy thought that mosquitoes brought the disease from decomposing matter and injected it into man and this was long before the discovery of pathogenic bacteria by Pasteur in 1857.

About the middle of the nineteenth century there was a remarkable development among German doctors and scientists in the study of helminths. Herbst in 1850 began the work of experimental parasitology when he fed trichinized meat to dogs and obtained the adult worms in his animals; Kückenmeister in 1852 discovered, by feeding experiments, that the "bladder worms" in rabbits were but a stage in the life cycle of tapeworms; in 1854–1856 he also showed that "bladder worms" in pigs were but a stage in the life cycle of human tapeworms; Virchow and Leuckart in the same decade determined the life cycle of *Trichinella* (*Trichina*) and Leuckart (1862) solved the mystery of hydatid cysts. All these and other experimental activities undoubtedly fired the minds and guided the thinking of the rising generation.

DISEASES DISCOVERED TO BE TRANSMITTED BY INSECTS

FILARIASIS: In 1863 Demarquay discovered a larval nematode in cases of chyluria; they were later seen by Wücherer in other cases, and Lewis (1872) discovered that the blood of man is the normal habitat of this filarial worm (*Filaria sanguinis hominis* of Lewis).

In 1866 Dr. Patrick Manson, a young medical man of imagination and unbounded energy, left the shores of his native country, England, and took up heroic work first at Formosa and later (1871) at Amoy, China. He investigated anything and everything that came his way, developing a remarkable ingenuity for interpreting old and solving new problems. He found filaria abundant in the blood of his Chinese patients, established the "periodicity" of their appearance in the peripheral circulation, and in 1879 published the first account of an insect, *Culex fatigans* (the house mosquito of the tropics), serving as the intermediate host in the developmental cycle of a parasite. Though Manson traced the developmental cycle from the intestine through the thoracic muscles, he did not determine how the parasites reached a new host. He believed at that time that the life of the mosquito was short, the females dying after laying their eggs, and so he formulated the theory that man was infected by drinking the water in which infected mosquitoes died. It was not till 1900 that the true method was discovered by Low. Manson's work was the real starting point of medical entomology. In 1890 Manson returned to London, engaged in the practice of medicine, and urged the development of tropical medicine. In 1893 he evolved his mosquito theory of malaria. Though he never had an opportunity to test his theory, he so impressed his ideas on Dr. Ronald Ross that the latter eventually made his epoch-making discovery in 1897–1898.

Only one other contribution by Manson can be recorded here. *Loa loa,* the African eye worm, was long identified both in America and Africa, but nothing was known of its life cycle. In 1891 Manson reported a new filaria in the blood of natives from the Congo and Old Malabar, naming it *Filaria sanguinis hominis major* (later known as *Microfilaria diurna*). On account of its diurnal periodicity Manson predicted that some bloodsucking, day-feeding fly would be found to be the intermediate host. From talks with the natives of Old Calabar he suggested that the "mangrove flies," *Chrysops dimidiata* and *Chrysops* spp., would prove the correct flies. In 1912 Leiper confirmed this prediction, and Kleine (1915) worked out the methods of transmission in detail.

Another remarkable discovery should be recorded here; it, in fact, antedated Manson's work. Fedschenko (1869) demonstrated that *Cyclops* spp. (Crustacea) were the intermediate hosts of the famous "fiery serpent" of Moses, the dragon worm, *Dracunculus medinensis* Linn. (hence the name of the disease, dracontiasis). Manson (1894) confirmed and extended the work of Fedschenko.

MALARIA: In 1880 Laveran, working in Algeria, discovered the parasite of malaria in the red blood cells of his patients. More than ten years passed before Laveran's organism was accepted as the causal agent of the disease. Though much had been learned about the parasite during this time, little progress was made till Manson evolved his mosquito theory and impressed it on Ronald Ross, a young British surgeon working in India. So farfetched appeared Manson's theory that he was dubbed "Mosquito Manson" by his distinguished medical confreres and regarded as rather fit for a lunatic asylum. Curiously enough, in 1883 an American physician, A. F. A. King, had also propounded a mosquito malarial theory, which, unfortunately, fell on deaf ears and unimaginative minds. Under Manson's urging Ross continued to work and in 1897 recorded his great discovery that "dappled-winged" mosquitoes served as the definitive hosts of species of *Plasmodium*. Ross's work was done under the most trying conditions and at a time when no one knew mosquitoes or their biology. His results were fully confirmed by Bastianelli, Bignami, and Grassi (1898, 1899), Manson (1898), and Sambon and Low (1900). This discovery by Ross is undoubtedly one of the great landmarks in medical history, for it has led to the reduction, and can lead to the elimination, of the most widespread and devastating of human diseases.

PIROPLASMOSIS: While the mosquito malarial theory came to fruition in India and Europe, Theobald Smith, working in Washington, D.C., discovered the causative agent of Texas or red-water fever of cattle, *Piroplasma bigemina,* a red-blood-cell-inhabiting protozoan. In 1893 Smith and Kilbourne published the results of their work. They demonstrated that the cattle tick, *Boophilus annulatus* Say, was the intermediate host. In addition, they showed that the parasite passes from the adult female ticks to their offspring and only young ticks (larvae) infect new hosts. This is the first instance of a protozoan passing by way of the egg to infect the young, which, in turn, transmit the disease to new hosts. Many other discoveries in the field of protozoan parasites of domestic animals have since been made and are of the greatest importance to animal husbandry. It would take us too far afield to discuss them here.

TRYPANOSOMIASIS: From about 1893 to the present time the most remarkable discoveries have been made in the field of insect-borne diseases. These can be reviewed only briefly. In 1895 Bruce discovered *Trypanosoma brucei,* the causative agent of nagana or tsetse fly disease of cattle in Zululand and demonstrated that the tsetse fly, *Glossina morsitans* Westw., could transmit the disease from the sick to the well. It was not, however, till 1909 that Kleine proved the developmental cycle in the fly and showed the true method of transmission. In 1901 Forde, in West Africa, observed a parasite in the blood of a European patient suffering from Gambian fever; later Dutton (1902) recognized it as a trypanosome and described it as *Trypanosoma gambiense* Dutton; Castellani (1903) and Bruce and Nabarro (1903) proved this trypanosome was the causative agent of sleeping sickness and that *Glossina palpalis* R.-D. was the transmitting fly. In 1910 Stephens and Fantham described *Trypanosoma rhodesiense* as the etiological agent of Rhodesian sleeping sickness, and Kinghorn and Yorke (1912) proved that *Glossina morsitans* Westw. was the transmitter. In South America Chagas (1909) demonstrated that a trypanosome, *T. cruzi,* was transmitted by a bug, *Triatoma megista* Burm. This parasite is the etiological agent of South American trypanosomiasis or what has been called Chagas' disease.

YELLOW FEVER: While these African investigations were being developed, the American Army Yellow Fever Commission, consisting of Reed, Carroll, Lazear, and Agramonte, made a still more remarkable discovery. They demonstrated (1900) that yellow fever can be transmitted only through the agency of the "tiger mosquito" or yellow-fever mosquito (*Stegomyia fasciata, Aedes calopus, Aedes argenteus*—now known as *Aedes aegypti*). Though Carlos Finlay, a Cuban physician, had as early as 1881 propounded a mosquito theory for yellow fever and had extensive experimental evidence in support of it, yet it must ever redound to the glory of this band of devoted workers that, because of their discoveries, one of the most deadly of human diseases could now be controlled or even eliminated. Though Noguchi (1919) announced that *Leptospira icteroides* was the etiological agent and his work was accepted by many workers, his results have since been abundantly disproved. It is now known to be caused by a recognized virus, which has been studied in great detail. For over a quarter of a century it was firmly believed that the only transmitter of yellow fever was the "tiger mosquito" and that man was the only animal susceptible to the disease. On this belief prophylactic measures against yellow fever were based, and remarkable results were obtained in reducing and controlling outbreaks of the disease. However, in 1928 two most important contributions were made to the yellow-fever problem. Stokes and his associates, working in West Africa, demonstrated that monkeys, *Macacus rhesus,* were susceptible to the disease, and since then many more species of monkeys, both from the Old World and the New World, have been shown to be susceptible to yellow fever. In the same year Bauer, working in the same laboratory, proved that three other species of mosquitoes were capable of transmitting yellow fever. Since that date over thirty additional species of mosquitoes have been shown to be capable of transmitting yellow fever.

In 1933 Soper and his associates reported an outbreak, in parts of Brazil, of what has been designated as jungle yellow fever. Since then large areas in South America have been shown to be endemic centers of this disease. Jungle yellow fever is identical with classical yellow fever, but its epidemiology is remarkably different. (See pp. 353–356.) These and other discoveries have thrown new light on the yellow-fever problem. The development of an effective vaccine by the workers of the Rockefeller Foundation in 1932 has provided one of the most efficient methods to prevent and reduce yellow-fever outbreaks.

PLAGUE: In 1894 Yersin and Kitasato independently discovered the causative agent of plague, *Pasteurella pestis,* and Yersin demonstrated that the disease in man was identical with a plaguelike disease of rodents. Simond (1898) suggested that fleas were agents in the dissemination of plague, and his experiments showed that he was on the right track. In 1903–1904 Verjbitski demonstrated that fleas act as vectors of the plague bacillus, but his results were not published till 1908. The development of the plague bacillus in the gut of the rat flea was independently discovered by Liston (1905), and the role fleas play in the epidemiology of plague was fully determined by the British Plague Commission (1906–1908). Finally Bacot and Martin (1914) demonstrated the method of transmission of the plague bacilli by fleas.

DENGUE: Dengue or breakbone fever, a disease of unknown etiology, was shown by Graham (1902) to be mosquito-borne, and his results were confirmed by Ashburn and Craig (1907). Though the mosquitoes with which these investigators were supposed to have worked have since been shown not to be true vectors, their discovery was of great importance. The true vectors have since been shown to be *Aedes aegypti* and *Aedes albopictus* (see pp. 357–358).

PHLEBOTOMUS FLIES AND DISEASE: Pappataci fever (three-day fever or sand-fly fever), another disease of unknown etiology, was shown by Doerr, Franz, and Taussig (1909) to be transmitted by a sand fly, *Phlebotomus papatasii* (Psychodidae). Oroya fever, verruga peruana, or Carrion's disease, a disease of rather high mortality in parts of South America, was demonstrated by Townsend (1913–1914) to be transmitted by *Phlebotomus verrucarum,* and his results have been confirmed by Noguchi and his associates (1929). *Phlebotomus* spp. have also been proved vectors of kala azar, Oriental sore, and espundia (diseases known as forms of leishmaniasis, the etiological agents being species of *Leishmania*), but at the present time (1949) many actual transmitters still remain unknown.

SPIROCHETAL DISEASES: In 1903 a peculiar disease of fowls caused by *Spirochaeta marchouxi* Nuttall was shown by Marchoux and Salimbeni to be tick-borne, the common fowl tick, *Argas persicus* Oken, being the vector. Various recurrent fevers of man caused by *Spirochaeta* spp. have since been shown to be tick- or louse-borne. Ross and Milne (1904) first demonstrated that the tick, *Ornithodorus moubata,* is the vector of African relapsing fever caused by *S. duttoni.* These conclusions were confirmed and extended by Dutton and Todd (1905) working independently in the Belgian Congo. Since then various species of ticks (*Argasidae*) and lice (*Pediculus humanus*) have been shown to be the natural transmitters of the different relapsing fevers of man. Mackie (1907), working in India, first demonstrated the part played by lice (*Pediculus corporis*) in the dissemination of relapsing fevers.

TSUTSUGAMUSHI DISEASE, KEDANI FEVER, FLOOD FEVER, OR JAPANESE RIVER FEVER: A serious disease in parts of Japan, China, Formosa, and other parts of the Far East, tsutsugamushi was first diagnosed as a distinct disease by Bälz and Kawakami in 1879. This peculiar disease had long been believed by the common people to be associated with the bites of a red mite. Bälz and Kawakami concluded there was no such association. Kitasato (1891–1893), however, decided that the bites of a red mite did play a role in the causation of the disease. The mite theory of the transmission of the disease has since been fully confirmed by the work of Tanaka (1899), Kitashima and Miyajima (1909, 1918), Miyajima and Okumura (1917), and others. The etiological agent was isolated by Nagayo and his associates (1930) and described as a rickettsia, *R. orientalis.* During World War II this disease was found to be widespread in many Eastern areas. The so-called "Mossman fever" of Australia, "scrub typhus" of Malaya and other parts of the East, and "pseudotyphoid" of Sumatra were found to be kedani fever and transmitted by mites (*Trombicula* spp; see pp. 110–113).

ROCKY MOUNTAIN SPOTTED FEVER: This peculiar disease prevalent in Montana and certain other Rocky Mountain states was definitely proved by Ricketts (1906) to be transmitted to man by a tick, *Dermacentor andersoni* Stiles (*venustus* Banks). His results have been fully confirmed by various later workers, and Wolbach (1916, 1919) determined the causative agent to be *Dermacentroxenus rickettsi* (Rickettsia bodies, so-called). This disease is now widespread in the United States (see pp. 73–74).

TYPHUS FEVER: Though the head and body lice (*Pediculus humanus* var. *capitis* and var. *corporis*) have been closely associated with man in all his long career, it was not till 1909 that Nicolle, Comte, and Conseil, working in

Tunis, demonstrated the role played by the body louse (*corporis*) in the spread of the much-dreaded typhus or jail fever. These results were confirmed by Ricketts and Wilder (1910) working independently in Mexico. Da Rocha-Lima (1916) discovered the causative agent and named it *Rickettsia prowazeki*. During World War I (about 1915) a peculiar disease dubbed "trench fever" appeared among the troops of the contending armies and was definitely proved by various workers to be disseminated by head and body lice (see p. 208). Töpfer (1916) designated what is considered the causal agent as *Rickettsia quintana*.

TULAREMIA: A peculiar plaguelike disease of rodents was investigated by McCoy (1911), and the etiological agent, *Bacterium tularense,* was isolated and described by McCoy and Chapin (1912). In 1911 Pearse, in Utah, described a peculiar disease of man under the title of "insect bites," and this disease later became known as "deer-fly fever." Francis (1919–1920) recognized the identity of "deer-fly fever" of man and the plaguelike disease of rodents and named the disease tularemia. Francis and Mayne (1921) demonstrated that the deer fly, *Chrysops discalis* (Tabanidae), was the transmitting insect. Since then a large number of insects and ticks have been shown to be able to transmit the disease in nature.

ONCHOCERCIASIS: Recent contributions in the field of medical entomology have been the solving of the life histories of *Onchocerca volvulus* Leuck. and *O. caecutiens* Brumpt (Nemathelminthes, family Filariidae). The former species occurs in Africa and the latter in parts of Central America and Mexico. Blacklock (1926) determined that *O. volvulus* passes part of its life cycle in black flies (*Eusimulium damnosum,* family Simuliidae) while Hoffman (1930) and Strong (1931) demonstrated that *O. caecutiens* undergoes a developmental cycle in at least three species of black flies. Both these round worms produce diseased conditions in man. These two species are now considered to be one and the same, *O. volvulus.*

In recent years several important diseases have been demonstrated to be insect-transmitted. Poliomyelitis, long associated with some bloodsucking insect as a vector, has been shown capable of being disseminated by filth-loving flies, as the housefly, blowflies, and flesh flies. How important a part these flies play has not been determined. St. Louis encephalitis, a new virus that appeared in epidemic form in St. Louis during 1933 and 1937 and has since been isolated in other parts of the country, has been shown to be disseminated to man by mosquitoes. The reservoir of this disease has been found in birds, primarily fowls, and in the fowl mite, *Dermanyssus gallinae.* Japanese B encephalitis, a serious disease in Japan and other parts of the East, has also been shown to be transmitted by mosquitoes. Equine encephalomyelitis (several different strains), primarily a disease of horses, appeared also in man in Massachusetts in 1938 and in California in the same year. In 1941 an extensive outbreak of human cases (over 3000) developed in the western prairie states of the United States and Canada. Mosquitoes have been proved to be the vectors of these diseases.

OTHER ASPECTS OF DISEASE TRANSMISSION

In the above survey nothing has been said of the mere mechanical carriage of pathogenic organisms by insects, especially filth-loving flies. Very early, flies, in the mind of the common people and the physicians, were associated with disease outbreaks. An abundance of flies during the summer presaged an unhealthy autumn, wrote Sydenham (1666), and since his time a long series of physicians and others have called attention to the abundance of and the dangers from filth-loving flies. Veeder (1898) called more specific attention to the housefly, and Reed, Vaughan, and Shakespeare (1900) outlined the role the housefly may play in the spread of typhoid fever. Since then the importance of filth-loving flies as possible disseminators of disease-producing organisms has been well established and recognized.

This brief historical survey will indicate, to some extent, the role insects play in the dissemination of human diseases. Had the writer attempted to include animal diseases other than those of man, the list would have been much extended and the importance of insects, from the point of view of human welfare, more strikingly portrayed. In addition, the role insects play as vectors of plant diseases has become, during the past fifty years, almost as important as that in animal diseases. Rand and Pierce gave an extended account of the subject up to 1920, and since then the so-called "mosaics," "chloroses," and other "virus" diseases of plants and their transmission by insects have assumed even greater significance.

In the gut of many insects are found representatives of the protozoan family Trypanosomidae, under the generic names *Crithidia, Herpetomonas, Phytomonas, Leishmania, Leptomonas,* and others of doubtful validity. The relationships of some of these forms to animal and plant diseases have been established, but the great majority of them remain undetermined. The problem of isolating, culturing these forms, and of determining their relation to the insects, to other animals, and to plants is extremely difficult. Progress has been made, and with the development of microtechnique we may expect much from the future.

FACTORS INVOLVED IN DISEASE TRANSMISSION

In the study of insect-borne disease, especially one in which the insect serves as the definitive or intermediate host, certain important considerations must always be kept in mind. Table 1 will serve to call attention to the more important features and indicate the far-reaching significance of the various factors involved. These factors are (1) the parasite or etiological agent; (2) the definitive host and the definitive reservoirs or nonreservoirs; (3) the method of transmission; (4) the intermediate host and the intermediate reservoirs or nonreservoirs; and (5) the method of transmission. The significance of these facts can be best illustrated by giving several examples.

Table 1. Three diseases and the factors involved in their transmission.

	Malaria	Yellow fever	Sleeping sickness
Parasite (etiological agent)	*Plasmodium vivax* *P. malariae* *P. falciparum*	Virus	*Trypanosoma gambiense*
Definitive host	*Anopheles* spp. How many?	*Aedes aegypti* and many other spp. of mosquitoes. How many more?	*Glossina palpalis* *Glossina* spp. (How many?)
Definitive host reservoirs	?	All not definitely known	Game animals?
Method of transmission	Sporozoites Inoculative	? Inoculative	Infective salivary trypanosomes Inoculative
Intermediate host	Man Other animals?	Man Monkeys Other animals?	Man Domestic cattle?
Intermediate host reservoirs	Man with gametocytes in his blood Other animals?	Monkeys Other animals?	Domestic cattle Game animals?
Method of transmission	Male and female gametocytes Ingested	?	Certain infective blood types of the trypanosome Ingested

Examining such an outline, one is immediately struck by the lacunae, even in some of the best-known insect-borne diseases. In malaria it is apparent that the only definitive host reservoirs are mosquitoes (*Anopheles* spp.), but how long they can remain infected is still a matter of uncertainty. The number of *Anopheles* species that can act and the conditions under which they may serve as definitive hosts are still not well known, though much progress has been made toward solving these problems. In yellow fever the etiological agent (parasite) is a virus; only recently have the animal reservoirs been determined and, as yet, not all the mosquito transmitters have been recognized. Many factors in the problem of sleeping sickness remain unsolved. In a similar manner, data on all the insect-borne diseases could be assembled and the numerous unsolved problems pointed out.

The literature dealing with medical entomology, parasitology, and preventive medicine has become of vast proportions, especially during the past fifty years. In each field, and we should include bacteriology and veterinary medicine, the entomologist will find texts, journals, reviews, summaries, etc., that he must consult if he is to keep abreast of the times. In addition to the references given at the end of each chapter, I am appending to this chapter a list of the more important journals, reviews, summaries, and other publications that the entomologist should consult. In many of the texts listed will be found bibliographies, some of them very extensive, and they should be of great benefit to those who desire to explore beyond the outer doorway.

DEFINITION OF SOME OF THE TERMS EMPLOYED ABOVE

Definitive Host. The host in which the sexual life of the parasite is passed.

Intermediate Host. The host in which the asexual stages of the parasite are passed.

Definitive Host Reservoir. Hosts in which a natural supply of the sexual stage of a parasite occurs.

Intermediate Host Reservoir. Hosts in which a natural supply of the asexual stages of a parasite occurs. (In using these two terms the word *host* is frequently omitted.)

Transmission. The passage of a parasite from the intermediate host to the definitive host or vice versa.

Contaminative. Infection or transmission is said to be contaminative when the pathogenic organism gains entrance by way of abrasions, by fecal wastes deposited on the skin, etc.

Inoculative. This term is applied when invasion of an organism takes place through the act of biting, the organism being inoculated during the feeding process.

Ingestive. This applies when parasites are obtained at the time of feeding, the infective stage being ingested *per os.*

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[1] Now known as the National Institute of Health.

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CHAPTER II

The Arthropoda

THE Arthropoda constitute the largest of the animal phyla. They are bilaterally symmetrical animals. The body is divided into rings or segments of which several or many bear jointed appendages. They possess an exoskeleton composed mainly of chitin. During growth the external skeleton is periodically molted in its entirety. The nervous system consists of a pair of ganglia to each segment, the ganglia being connected longitudinally and laterally by commissures. It is located below the gut and forms a collar about it in the head where the brain is located. The blood circulatory system consists of a longitudinal dorsal vessel or heart. It is perforated and contractile, the pulsations usually proceeding from the posterior to the anterior end. There is no closed system of blood vessels, the blood flowing freely about the internal organs.

CLASSIFICATION OF THE ARTHROPODA

The phylum is divided into a rather large number (about thirteen) of classes. Only five of these are of interest to the student of medical entomology. Four of the five classes will be dealt with in some detail in the following chapters. In order not to burden the text with too much morphological detail the main structures of each class will be given under the discussion of the group. The following key will aid in separating the main classes of the Arthropoda:

1. With two pairs of antennae and usually at least five pairs of ambulatory legs; respiration by means of blood gills; all aquatic or semi-aquatic .... *Crustacea*
2. Without antennae; with only four pairs of ambulatory legs; respiration aerial by means of trachea or the surface of the body. (Scorpions, spiders, mites, etc.) .... *Arachnida*
3. With only one pair of antennae; respiration aerial 4
4. With only three pairs of legs and usually with wings in the adult state.

(Insects) .... *Hexapoda*

With more than three pairs of legs; wings absent 5

5. With two pairs of legs on many of the body segments. (Millepedes). .... *Diplopoda*

With one pair of legs on each of the body segments. (Centipedes). .... *Chilopoda*

THE CLASS CRUSTACEA

The Crustacea constitute a large class of almost exclusively aquatic animals. They occupy ponds, lakes, and streams and are the dominant form of animal life in the sea. Some species, such as sow bugs and pill bugs, are terrestrial and are generally found in damp situations. The more common representatives are the crayfishes, lobsters, shrimps, water fleas, etc. In the waters of the world they play a part closely parallel to that which insects play on the land. The great majority are free-living, feeding on aquatic plants, preying on animals, and performing the important function of scavengers of the waters. Like insects, many species are represented by enormous numbers of individuals, and the waters teem with their countless millions. The minute Crustacea furnish the main food for the larger aquatic animals. Despite their numbers and abundance, comparatively few species are known to play a part in the transmission of human parasites.

BRIEF SYNOPSIS OF THE CRUSTACEA

The class Crustacea is divided into two subclasses, the Entomostraca and the Malacostraca. Both of these subclasses contain a few species that serve as intermediate hosts of human parasites.

THE SUBCLASS ENTOMOSTRACA: This subclass contains an immense number of small marine and fresh-water forms. Most of them are free-living, though some lead a parasitic life. They are of great importance since they constitute the main food supply of the larger aquatic animals, especially the fishes. This subclass is divided into four orders—Phyllopoda, Ostracoda, Copepoda, and Cladocera. Although representatives of all these orders serve as intermediate hosts of animal parasites, only the members of the Copepoda have been so far involved in human infections.

THE SUBCLASS MALACOSTRACA: This group contains the larger Crustacea such as the lobsters, crayfishes, and crabs. It is divided into a number of orders, of which only the Decapoda are known to act as intermediate hosts of human parasites.

CRUSTACEA AND HUMAN DISEASE

A few of the Crustacea bear an important relation to human diseases. Certain of them act as secondary or intermediate hosts of human parasites. *Dracunculus medinensis,* the Guinea worm, passes its larval stage in various species of copepods [1] belonging to the genus *Cyclops* (Fig. 1). Man and other animals become infected by drinking raw water containing parasitized *Cyclops* spp. This disease has been known from antiquity, and Moses referred to it as "the fiery serpent." When infected *Cyclops* spp. are swallowed, the larvae of *Dracunculus medinensis* escape and penetrate the wall of the stomach or intestine. They migrate through the tissues, lodging at last in the subcutaneous connective tissue. It requires from 10 to 14 months for the females to reach maturity. The females measure from 70 to 110 cm. in length. When mature the females produce blisterlike lesions on the lower extremities as the feet and ankles (Fig. 2) and also on other parts of the body. The breaking of these lesions enables the parasites to discharge their young—small filarial worms. These are discharged whenever the infected member comes in contact with fresh water. Dogs, horses, cattle, and other animals serve also as hosts of this parasite and undoubtedly aid greatly in its spread and prevalence in any region where it has become established. Owing to the fact that no clinical symptoms appear until the females are mature and that there is no known method of early diagnosis, persons harboring this parasite may unknowingly spread it from one region to another.

The presence of this worm causes no symptoms of disease until the formation of the lesions. Then occurs intense itching followed by nausea, vomiting, diarrhea, severe dyspnea, and giddiness. These conditions are supposed to be due to the toxic secretions of the worm.

The Guinea worm is widely distributed. It occurs over vast areas in Africa, Iran, India, southern Russia, the islands of the Caribbean Sea, the Guianas, and parts of Brazil. It is also found in North America in fur-bearing animals such as foxes, raccoons, minks, and dogs. There is no effective treatment except the removal of the worms. Prophylaxis consists in drinking only boiled or filtered water and in preventing infected persons from coming in contact with water used for drinking purposes.

Another important human parasite, *Diphyllobothrium latum,* the broad fish tapeworm, has become well established in certain sections of North America. The early larval stages of this parasite develop in certain fresh-water Crustacea of the genera *Cyclops* and *Diaptomus*. These infected crustaceans are eaten by plankton-feeding fishes such as pike, pickerel, and turbot. Within the fish the parasitic larvae escape and penetrate through the wall of the stomach. In the course of a few days these larvae imbed themselves in the fleshy tissues, where they remain in a sort of encysted condition (plerocercoids). Man becomes infected by eating partially cooked or raw fish. The tapeworm becomes mature in from five to six weeks after the ingestion of the larva by man.

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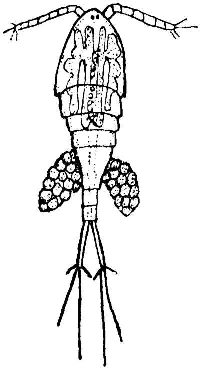
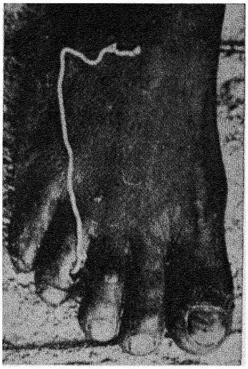
[1] These are frequently called "water fleas," a term that is restricted to the cladocerans (*Daphnia* and its allies).





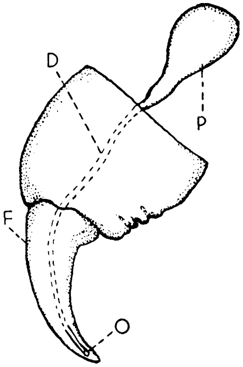


Fig. 1 (*left*). *Cyclops* sp., with eggs attached.

Fig. 2 (*center*). Guinea worm partially extracted from the fourth toe. (From Castellani and Chalmers, *Manual of Tropical Medicine.*)

Fig. 3 (*right*). Chelicera of a spider, somewhat diagrammatic. D, duct from poison gland; F, fang; O, opening of poison gland; P, poison gland.

This parasite is widely distributed in Europe, parts of Africa, and in Siberia, Japan, and Manchuria; it is well established in central North America. The plerocercoids have been found in fishes from most of the large lakes of the Canadian prairies, from lakes in northern Minnesota and northern Michigan, and from the Greak Lakes as far east as Lake Erie. As cats, dogs, foxes, bears, and probably other fish-eating animals, as well as man, are hosts of the adult tapeworm, the widespread distribution of this parasite is assured.

In man the tapeworm causes a rather serious disease. The clinical symptoms are those of severe anemia, reduced hemoglobin and general weakness. Prophylaxis consists in the thorough cooking of all fish intended for food.

The lung fluke, *Paragonimus westermani,* passes part of its larval life in fresh-water crayfishes and crabs. The adults are found in the lungs of man, cats, dogs, foxes, wolves, pigs, and many other animals. It occurs principally in the Far East (Japan, Korea, Formosa, French Indo-China, Siam, Federated

Malay States, Bengal, Assam, Madras, and the Philippines) and is recorded from parts of Africa, the Dutch East Indies and in certain areas of South and Central America. The life cycle of the fluke is rather complicated, involving a snail (a species of the genus *Melania*) and then a fresh-water crayfish or crab. Man becomes infected by eating the raw flesh of these animals. The nature of the diseased condition produced by this worm in man depends on the localization of the parasite. Though normally a parasite of the lungs, it may invade various organs, even the brain. As no effective treatment appears to be known, it would seem imperative that only thoroughly cooked meat of fresh-water crayfishes and crabs should be eaten.

Table 2. Interrelation of Crustacea and human parasites.

Parasite	Organ attacked	Primary hosts	Intermediate hosts	
			First	Second
Dracunculus medinensis (Guinea worm)	Migrates through subcutaneous tissues	Man, cats, monkeys, dogs, foxes, etc.	*Cyclops bicuspidatus* *C. coronatus*	None required
Diphyllobothrium latum (broad fish tapeworm)	Intestine	Man, cats, dogs, foxes, bears, pigs, mink, etc.	*Cyclops strenuus* *Diaptomus oregonensis* *D. vulgaris* *D. gracilis* *D. graciliodes*	*Esox lucius* *Stizostedion vitreum* *S. canadense* *S. griseum* *Lota maculosa* *Perca flavescens* and many others
Paragonimus westermani (lung fluke)	Lungs and occasionally other organs	Man, cats, dogs, wolves, pigs, beavers, tigers, etc.	*Melania libertina* *Melania* spp. (snails)	*Astacus japonicus* *A. similis* *Potamon dehaani* *P. obtusipes* and others

THE CLASS ARACHNIDA

Scorpions, Pseudoscorpions, Spiders, Mites, Ticks

The Arachnida are air-breathing arthropods. The body is usually divided into two regions—the cephalothorax, including the fused head and thorax, and the abdomen. The abdomen may be either segmented or unsegmented. In the mites and ticks the entire body is fused and forms a kind of sac. The head appendages are highly modified. The antennae are lacking and the eyes, when present, are rather simple and sessile. In the adults there are four pairs of ambulatory legs and these are attached to the cephalothorax. The first stage or larva has only three pairs of legs. The organs of respiration, when present, consist of either tracheae or book lungs. The sexes are distinct and the metamorphosis is incomplete, the young closely resembling the adult.

The arachnids suck the juices[2] of their victims by means of a sucking stomach. The mouth parts are adapted either for crushing their prey and sucking up the liquid portions or for piercing and cutting the tissues of their hosts (parasitic forms) in order to obtain blood. The mouth parts consist of a pair of *chelicerae*[3] located in front of the mouth opening; a pair of *pedipalpi,* the palpi or palps, situated either at the sides of the mouth or immediately behind it; and, in many forms, a peculiar structure known as the *hypostome.* The hypostome is most highly developed in some of the parasitic forms and is fully discussed later. It is located, when present, directly beneath the mouth opening. The structure of the chelicerae varies greatly in the different orders of the Arachnida. In the spiders (Araneida) each chelicera consists of a large basal segment and a terminal clawlike one (Fig. 3). By means of these appendages the spider seizes and kills its prey. Near the tip of the claw is the opening of the poison gland. In the parasitic forms (ticks, etc.) the chelicerae are modified to serve as cutting and piercing organs. They are fully discussed and illustrated in the following chapter. The pedipalpi are more or less leglike in all the groups and consist of four to six segments. In the spiders the pedipalpi[4] of the male are greatly modified into very specialized organs for the transference of the semen to the females. In many of the ticks they serve as organs for the protection of the highly developed piercing organs.

SYNOPSIS OF THE ARACHNIDA

The class Arachnida is divided into nine to twelve orders. From the standpoint of the medical workers, only six of these orders are known to be of importance. Of these six, only one, the Acarina, is of sufficient importance to be treated in any detail. The other five contain forms which possess poison glands. Their bites or stings, when they do attack humans, may be of such severity as to require medical attention. Certain of these forms are treated in a brief chapter (Chapter XIX) dealing with the poisons of arthropods.

The following key will aid in separating the more common orders of Arachnida.

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[2] The solpugids and the harvestmen (daddy longlegs) are supposed to take solid food.

[3] The chelicerae are homologous to the second antennae of the Crustacea and have become modified into prehensile or cutting organs; the true antennae, the first antennae of Crustacea, are lost in the spiders. In insects the true antennae are retained but the second antennae are lost.

[4] For an extended account see Comstock, *The Spider Book* (1948).

1. Abdomen distinctly segmented 2
   Abdomen not distinctly segmented 4
2. Abdomen armed with a taillike prolongation. (Scorpions) .... *Scorpionida*
   Abdomen without a taillike prolongation 3
3. Palpi chelate or with pincerlike claws. (Pseudoscorpions) ....
   .... *Pseudoscorpionida*
   Palpi not chelate or without pincerlike claws .... *Pedipalpida*
   .... *Solpugida*
4. Abdomen joined to the cephalothorax by a short, narrow stalk. (Spiders) .... *Araneida*
   Abdomen fused with the cephalothorax, forming a saclike body .. *Acarina*

THE ORDER ACARINA

The Acarina are rather small to minute arachnids. The largest, such as some fully gorged ticks, may reach a length of nearly 25 mm., while the smallest rarely exceed 0.25 mm. in length. The order contains a large number of species. Like the insects and crustaceans, the species are noteworthy for the vast number of individuals. The body is depressed dorsoventrally and is undoubtedly an adaptation for their mode of life. The head, thorax, and abdomen are fused, giving them a saclike appearance. In some cases the cephalothorax may be demarcated from the abdomen by a groove or furrow. The body may be partially or completely covered by a scutum or shield. The mouth parts are located either anteriorly or on the anterior ventral surface. These structures are described in detail in the discussion of the various orders of mites. Eyes are either present or absent; when present they consist of simple convex facets and are generally located on the margin of the scutum or on folds on the ventral surface. The respiratory organs, when present, consist of tracheae connected to the exterior by means of spiracles. The spiracles are usually located on chitinized plates and may be either in pairs or singly. Some groups, as the sarcoptic and demodectic mites, lack tracheae, the animals breathing directly through their body wall. The sexes are distinct, the males generally smaller than the females. The opening of the reproductive organs is located on the ventral surface, usually directly behind the mouth parts. The digestive system consists of a straight tube, often supplied with numerous tubular branches. The anal opening is either ventral or dorsal, rarely terminal.

The mites exhibit a great variety of habits. They live principally on fluid nutriment, which is obtained from living plants or animals or from decaying organic matter. Many are free-living and predaceous, and large numbers are parasitic. The parasitic mites are of great interest on account of the wide variety of their habitats. Many, like the ticks, are external parasites of animals, feeding on the blood of their hosts; some, like many Sarcoptidae and Demodicidae, burrow in the skin of their hosts and cause severe itching and diseased conditions; others, such as *Halarachne* spp. and *Pneumonyssus* spp., are found in the lungs of seals and Old World monkeys, respectively; some, like the species of Trombidiidae, are parasitic in their larval stage (chiggers) but invariably free-living and herbivorous or predaceous as nymphs and adults. Many species attack birds and feed on the scales and feathers or even invade the lungs, air sacs, and hollow bones (as *Cytoleichus nudus*); while others, such as the Tyroglyphidae, feed on stored food products, and man may be attacked by them when handling such material. Of still greater importance has been the discovery that many bloodsucking mites may serve as intermediate hosts of various pathogenic organisms of man and animals. In recent years the part played by the Acarina in the transmission of pathogenic organisms of man and animals has been studied by numerous investigators, and brief accounts of this work will be found under the discussion of the various groups.

BRIEF SYNOPSIS OF THE ACARINA

The Acarina is divided into a number of suborders (usually eight), based largely on the structure of the respiratory system. Five of these suborders contain mites that are known to be parasitic and have some relation to man either as direct agents in producing diseased conditions or as vectors of pathogenic organisms. The classification of the order is far from satisfactory, but the following key will aid the student in placing parasitic forms:

KEY TO THE SUBORDERS AND SUPERFAMILIES OF PARASITIC ACARINA[5]

1. Body vermiform, much prolonged behind; distinctly annulate or ringed; legs rudimentary and apparently composed of only three segments; parasitic in the hair follicles or sebaceous glands of mammals .... Suborder BRACHYPODA

There is only one superfamily .... *Demodicoidea*

Body not vermiform, not prolonged behind; not parasitic in the hair follicles or sebaceous glands of mammals 2

2. Tracheae present; spiracular openings two, one on each side of the body usually above the third or fourth coxa or a little behind them; spiracles

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[5] There are more recent classifications, but this is more easily understood and should meet the needs of most workers in medical entomology.

opening through distinct stigmatal plates ...... Suborder MESOSTIGMATA

2a. Hypostome large, furnished beneath with numerous recurved teeth; venter with furrows; skin leathery; large forms. (The ticks) .... Superfamily *Ixodoidea*

2b. Hypostome small without recurved teeth beneath; venter without furrows but often with coriaceous shields .... Superfamily *Parasitoidea*

Tracheae, when present, not opening through lateral spiracles 3

3. Tracheae usually present, the spiracular openings near or at the bases of the chelicerae; larvae frequently parasitic, the adults free-living .... Suborder PROSTIGMATA

3a. Last segment of the palpus never forms a "thumb" to the preceding joint; body with few hairs .... Superfamily *Eupodoidea*

3b. Last segment of the palpus forms a "thumb" to the preceding joint, which ends in a claw .... Superfamily *Trombidoidea*

Tracheae, when present, not opening at the bases of the chelicerae 4

4. Tracheae present; body divided into cephalothorax and abdomen, and the abdomen shows evidence of segmentation; females with a clavate hair between the first and second pair of legs ...... Suborder HETEROSTIGMATA

This suborder contains one superfamily .... *Tarsonemoidea*

Tracheae absent; no division between cephalothorax and abdomen; abdomen without true segmentation; females never with a clavate hair between the first and second pair of legs .... Suborder ASTIGMATA

4a. Surface of the body with fine parallel lines or folds; tarsi often provided with stalked suckers; parasitic in all stages, chiefly on vertebrates .... Superfamily *Sarcoptoidea*

4b. Surface of the body without fine parallel lines or folds; tarsi without stalked suckers; adults never true parasites .... Superfamily *Tyroglyphoidea*

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CHAPTER III

The Order Acarina; Ixodoidea

THE ticks constitute the superfamily Ixodoidea. They are readily distinguished from all other mites by the possession of a pair of stigmatal plates (Figs. 4,5) situated laterally above, and usually posterior to, the fourth pair of legs. Furthermore their large size and leathery skin distinguish them from all other mites. The superfamily consists of two families—the Ixodidae, in which the species are recognized by the presence of a dorsal shield or scutum and the capitulum is located at the anterior margin and is visible from the dorsal surface, and the Argasidae, in which the dorsal shield is absent and the capitulum is ventral and rarely visible from the dorsal view (Figs. 12–14). The capitulum is a specialized organ and its structure is the most characteristic feature of

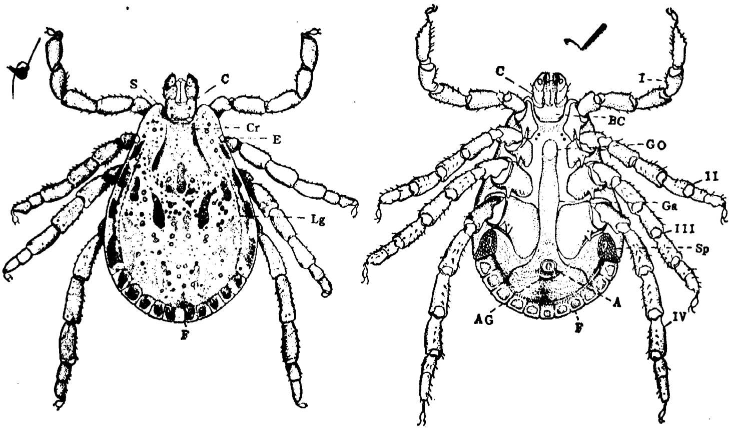

Fig. 4. Dermacentor andersoni. Left: Dorsal view of male. *Right:* Ventral view of male. A, anus; AG, anal groove; BC, basis capituli; C. capitulum; Cr, cervical groove; E, eye; F, festoons; Ga, genital groove; GO, genital opening; Lg, lateral groove in scutum; S, scapula; Sp, spiracle; I–IV, the legs.

ticks. The group is not a large one in number of species. Probably not more than four hundred are known at present. In number of individuals, ticks are often very abundant, and constitute one of the most important groups of animal ectoparasites and vectors of diseases. All ticks are parasites of vertebrates and are most abundant on mammals and reptiles, though they are also common on birds and amphibia. Their food consists entirely of blood and lymph taken from their hosts. The life cycles of the various species of ticks differ greatly, some requiring only a single host, whereas others drop from their hosts after each feeding or remain on their hosts for two feedings and then drop off (Fig. 20). Owing to their elastic, leathery skins, ticks, especially those belonging to the family Ixodidae, can engorge an enormous amount of blood and increase greatly in size (Fig. 23). In general, ticks vary in size from less than 2 mm. to nearly 25 mm. (some fully gorged females).

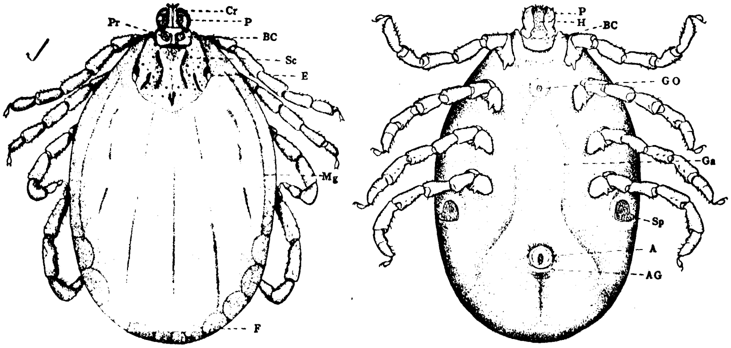

Fig. 5. Dermacentor andersoni. Left: Dorsal view of female. *Right:* Ventral view of female. A, anus; AG, anal groove; BC, basis capituli; Cr, chelicera; E, eye; F, festoons; Ga, genital groove; GO, genital opening; H, hypostome; Mg, marginal groove; P, palpus; Pr, porose areas; Sc, scutum; Sp, spiracle.

Ticks are widely distributed throughout the world but are most abundant in the tropics and subtropics. Only two species, *Ornithodoros moubata* and *O. rudis,* are primarily restricted to man. Man is, however, used intermittently as a host by a rather large number of species. In recent years ticks have been shown to be the intermediate hosts and distributors of a large number of very important diseases of man and of domestic and game animals. Furthermore, tick bites are known to produce rather serious effects, even death, in man and animals (lambs and calves, etc.). On account of these complicated interrelations ticks have become very important factors in public health and human welfare.

MORPHOLOGY OF TICKS

EXTERNAL ANATOMY

THE IXODIDAE: The external structures of ticks are primarily adapted to meet the needs of parasitic life. The body is saclike, there being no divisions between the head, thorax, and abdomen (Figs. 4,5). It is somewhat depressed dorsoventrally, especially so in the unengorged tick and in the early stages. The body bears on the dorsum a shield or scutum, which varies in size and shape according to the species. In the female the shield is small, but in the male it almost covers the entire dorsal surface (Figs. 4,5). The eyes, when present, are located on or near the margin of the anterior half of the scutum (Figs. 4,5 E). There are four pairs of legs (in the larvae only three pairs are present).

THE CAPITULUM. Located in an emargination, the camerostome, at the anterior end of the body is the specialized head, false head, or capitulum (Figs. 4,6). The basal portion, basis capituli (BC), consists of a rather broad, dense, sclerotized ring, constricted somewhat posteriorly to form a neck that fits into the anterior opening of the body cavity. Within and extending beyond the ring are the essential mouth parts concerned in piercing the host and extracting blood. The basis capituli varies in shape in the different genera of ticks; it may appear from the dorsal view as hexagonal, rectangular, or even triangular and may bear ridges, sharp angles, or other distinguishing characteristics. Females have a pair of depressions on the dorsal surface of the basis capituli. In these depressions lie the porose areas (Fig. 5 Pr), which consist of numerous open pores. They are of considerable taxonomic value, but their exact function is not known.

THE PALPI OR PEDIPALPI: These structures arise from the lateroventral margin of the basis capituli. Each palpus consists of four segments (Fig. 6). The first segment is usually very short and not easily recognized when the capitulum is examined from the dorsal side. The second and third segments are longer, and the fourth segment is located in a deep pit or depression on the third. The fourth segment is usually furnished with a crown or row of stiff hairs, which may have a sensory function. In many of the Ixodidae the palpi are grooved along their inner face and form shields for the chelicerae and hypostome. The margins of the grooves are commonly supplied with long or short spines of various shapes (Fig. 6).

THE HYPOSTOME: A dartlike structure, the hypostome (Fig. 6 Hph), arises from the median ventral surface of the basis capituli and protrudes forward directly beneath the mouth opening (Fig. 7 Hp). It consists of a basal portion, which is smooth and convex ventrally, and a distal portion, the ventral surface of which is provided with longitudinal rows of backward-projecting teeth. It is divided by a median fissure so that the teeth are separated into two series of files. The number of rows of teeth and the number of teeth in the rows differ in the various species and provide good characters for identification. The hypostome, when embedded in the tissues of the animal, acts as an effective anchor in maintaining the position of the tick. In fact, unless great care is exercised in removing ticks, the hypostome is frequently left in the host or a portion of the host's skin is removed with the tick.

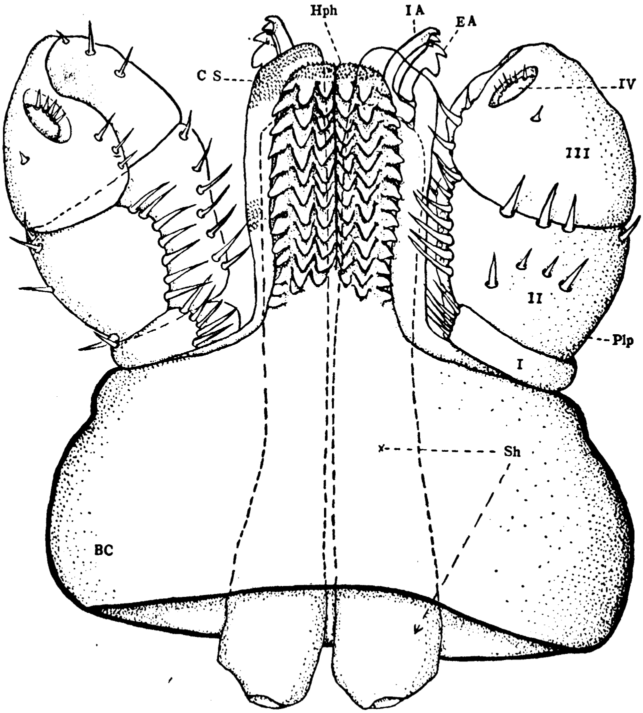

Fig. 6. Ventral view of capitulum of *Dermacentor andersoni.* BC, basis capituli; CS, cheliceral sheath; EA, external article; Hph, hypostome; IA, internal article; Plp, palpus (I–IV, segments of palpus); Sh, shaft of chelicera.

THE CHELICERAE: The chelicerae are the most important cutting organs of the mouth parts, and their structure is complicated. They arise directly above the mouth opening and consist of a pair of cylindrical shafts, each lying within its sheath, the so-called "cheliceral sheaths" (Figs. 6,8). The sheaths arise as prolongations of the anterior margin of the basis capituli and lie in close contact with each other. The distal extremity of each sheath forms a flexible membrane, which invaginates and is attached to the chelicera directly behind the digits or articles (Fig. 8 CS). In this way the sheath forms a protection for the digits when they are withdrawn. The outer surface of the sheath, except the basal part, is usually covered with minute denticles, which give it the appearance of a fine file. Each chelicera, the so-called "mandible," consists of a cylindrical shaft that bears at its extremity the chelate digits (Figs. 6,8). The shaft is very long and projects backward beyond the basis capituli into the body. The proximal part is dilated and to it are attached the retractor muscles of the chelicerae. The distal portion is more heavily sclerotized and bears at its extremity the digits or articles (Fig. 8). The articles are usually two in number: an internal digit with sharp cutting teeth articulated directly with the shaft and activated by two powerful tendons—an internal one and an external one—arising from the mass of muscles within the shaft, and an external digit articulated with the internal digit and provided with sharp, pointed cusps. It is these organs that cut and lacerate the tissues of the host. A brief account of the method of feeding is given later.

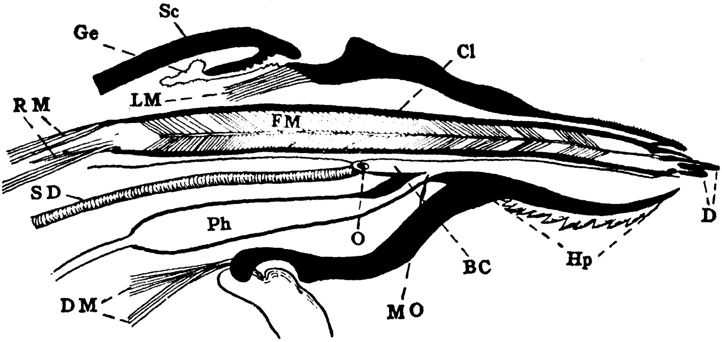

Fig. 7. Median longitudinal section through the capitulum of a tick to show the relations of the internal and external parts. BC, buccal cavity; Cl, chelicera; D, digits of chelicera; DM, depressor muscles of capitulum FM, flexor muscles of the digits; Ge, Gené's organ; Hp, hypostome; LM, levator muscles of capitulum; MO, opening into pharynx; O, opening of salivary duct; Ph, pharynx; RM, retractor muscles of chelicera; Sc, scutum; SD, salivary duct. (Diagrammatic; after Nuttall and Warburton, modified.)

THE BODY: The dorsal portion of the body bears a scutum or shield. In the males the scutum covers practically the entire body surface (Fig. 4); in the females (Fig. 5) the scutum varies greatly in size and shape so that it serves as a means of distinguishing the different species. It never covers more than a small part of the dorsal surface. The scutum may be ornamented or plain (Figs. 4,5,9), and it bears furrows or grooves. The anterior margin is usually deeply emarginate; the lateral angles project forward and are called the scapulae (Fig. 4 s). On the dorsal surface of the scutum and body are several grooves that are of considerable significance. These are: (1) the cervical grooves that extend from the inner angles of the scapulae backwards on the scutum (Fig. 4 Cr); (2) lateral grooves that extend along the sides of the scutum in the males (Lg); (3) marginal grooves, extending longitudinally near the lateral margins of the body in the females (Fig. 5 Mg). The scutum may be marked with shallow or deep punctures. On the sides of the scutum, either on the edge or just inside it, are the eyes, small globular elevations (Figs. 4,5). In many ticks the eyes are lacking.

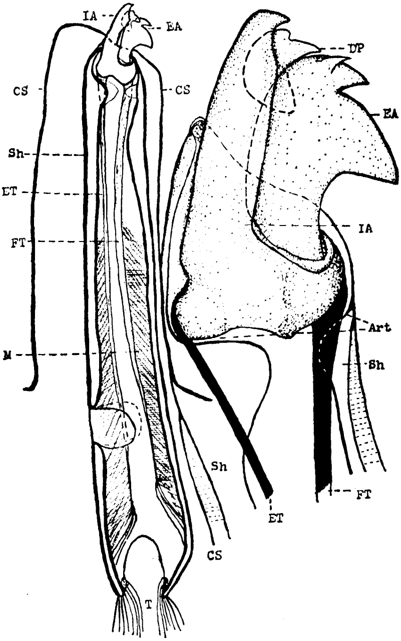

Fig. 8. Dermacentor andersoni. Left: A single chelicera, ventral view. *Right:* Tip of chelicera greatly enlarged to show the articles, ventral view. Art, points of articulation of the internal article with the cheliceral shaft; CS, cheliceral sheath; DP, dorsal process of internal article; EA, external article; ET, retractor tendon of internal article; FT, flexor tendon of internal article; IA, internal article; M, muscles, Sh, shaft of chelicera; T, tendons of retractor muscles of chelicera.

The ventral surface presents some important structures. The legs are prominent features and are numbered I, II, III, and IV (Fig. 4), beginning at the anterior end. Directly behind the basis capituli will be found the opening of the genital organs in both the males and females (Figs. 4,5 GO).[1] Extending

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[1] The genital opening is usually located between the first or second pair of legs, though in the genus *Ixodes* it is found between the third pair of legs.

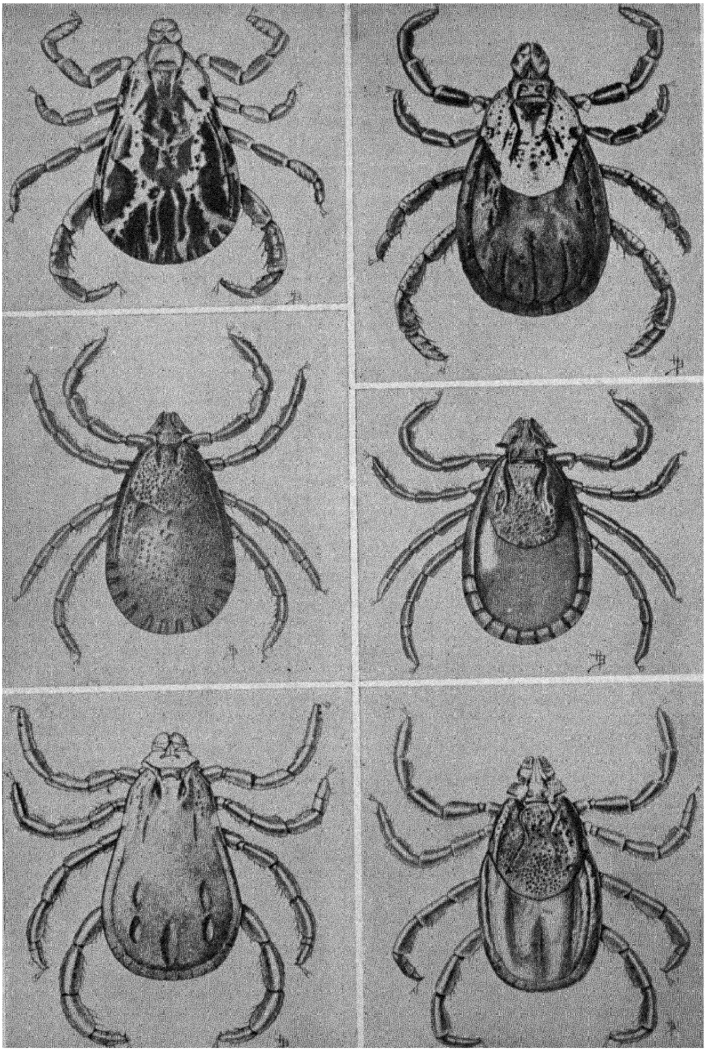
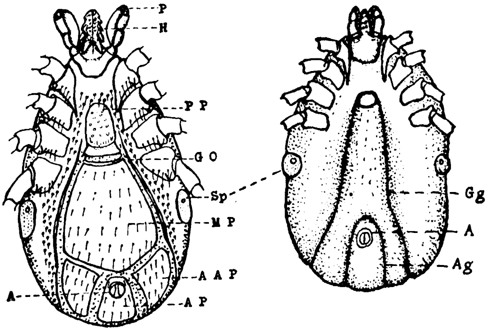


Fig. 9. Ticks. *From the top down: **Dermacentor variabilis,*** the dog tick; ***Haemaphysalis leporis-palustris,*** the rabbit tick; ***Rhipicephalus sanguineus,*** the brown dog tick. Males are at the left, females at the right. (After the U.S. Bureau of Entomology.)

backwards from the genital orifice are a pair of grooves, the genital grooves (Figs. 4,5 Ga). These curving grooves extend to the posterior margin in nearly all species. Between the genital grooves in the median line and usually far behind the fourth pair of legs is the anal opening. Directly behind the anal opening is the anal groove, the convexity directed backward. This groove is present in all species of the Ixodidae except in the genera *Boophilus* and *Ixodes*. In *Boophilus* the groove is lacking, whereas in *Ixodes* the groove surrounds the anus in front (Fig. 10). On the ventral surface of the males of the genera *Ixodes, Boophilus,* and *Rhipicephalus* there are various types of sclerotized shields. In *Ixodes* these shields or plates appear as nonsalient structures, and definite names have been applied to them (Fig. 10). In the other genera the plates are more or less raised and usually consist of two pairs, the adanal and accessory shields.



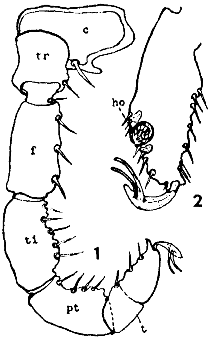


Fig. 10 (*left and center*). Ventral view of *Ixodes ricinus,* male; *Ixodes cookei,* female, ventral view. A, anus; Ag, anal groove; AP, anal plate; AAP, adanal plate; Gg, genital groove; GO, genital orifice; H, hypostome; MP, median plate; P, palpus; PP, pregenital plate; Sp, spiracle.

Fig. 11 (*right*). (*1*) Fourth leg of *Dermacentor andersoni.* (2) Tarsus of the first leg, showing Haller's organ (ho). c, coxa; f, femur; pt, protarsus t, tarsus, ti, tibia; tr, trochanter.

Behind and above the coxae of the fourth pair of legs are the spiracles. They are located on sclerotized stigmatal plates (Figs. 4,5,10). The stigmata are of various shapes, circular, oval, triangular, comma-shaped, etc. The spiracular openings are present in the nymphs and adults but are lacking in the larvae.

THE LEGS: Ticks, in the adult and nymphal stages, possess four pairs of legs. The larvae have only three pairs (Fig. 19). Each leg consists of the following parts: (1) The coxa. This is the basal portion and is firmly and immovably attached to the body wall. It is often armed with spines, spurs, or teeth (Fig. 11). (2) The trochanter. This is attached to the coxa by an intersegmental membrane. It is usually very short and has a somewhat rotatory movement in its socketlike depression in the coxa. (3) The femur. Following the trochanter is the stout, rather short femur. It is usually smooth or provided with a few hairs or spines. (4) The tibia. This is sometimes called the patella and is rather short and stout. (5) The protarsus. The tibia is followed by the protarsus. (6) The tarsus. The last segment, the tarsus, which is attached to the protarsus, has frequently a pseudoarticulation, indicating a two-jointed condition. (7) The claws. The tarsus bears the claws, which are located on a stalk. (8) The pulvillus. Lying between the claws is the pulvillus, which may be present or absent (Fig. 11).

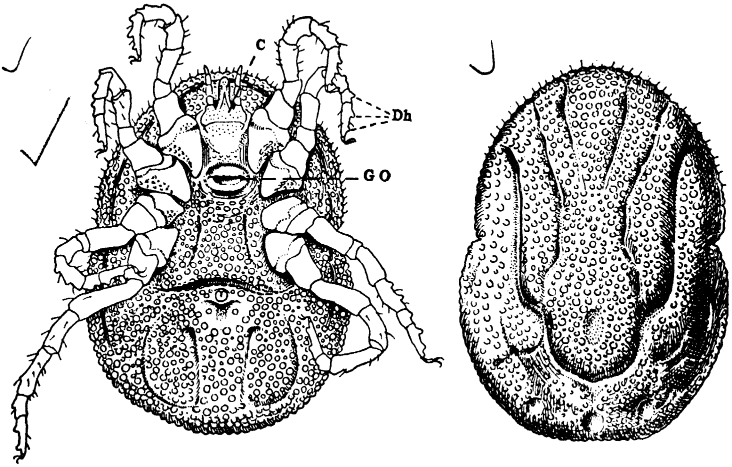


Fig. 12. Ornithodoros moubata. Left: Ventral view. *Right:* Dorsal view. C, capitulum; Dh, dorsal humps; GO, genital opening. (Redrawn from Nuttall and Warburton.)

On the tarsus of the first pair of legs is a peculiar organ (Fig. 11 ho) that should not be overlooked. This is the so-called Haller's organ. It consists of a small vesicle containing sensory hairs. Its cavity is connected with the exterior by a minute pore. Hindle and Merriam (1912) have definitely established that this organ has an olfactory function.

THE ARGASIDAE: The external anatomy of the Argasidae differs from that of the Ixodidae. The scutum or dorsal shield is lacking, and on this account the Argasidae have been called the "soft ticks." The capitulum is located on the ventral surface, just behind the anterior margin (Figs. 12,13). Porose areas are absent. The appearance of the dorsal surface of an argasid tick is markedly different from that of an ixodid tick. (Cf. Figs. 4,5 and 12–14.) The ventral surface possesses somewhat similar structures, but the arrangement of the grooves is often quite different (Fig. 14). The spiracles are located just above and in front of the fourth pair of coxae. The stigmatal plate is usually small and not so heavily sclerotized (Fig. 15). Eyes, when present, are ventral in position and are located on longitudinal ridges just above the coxae. Probably one of the most striking differences in the external anatomy is the leglike character of the pedipalpi or palpi (Fig. 16). These organs closely resemble the homologous structures in spiders and indicate the more generalized character of the argasid ticks. The structure of the legs is similar to that of the Ixodidae except that the pulvillus is very small or lacking and the coxae are unarmed (without spines or teeth).

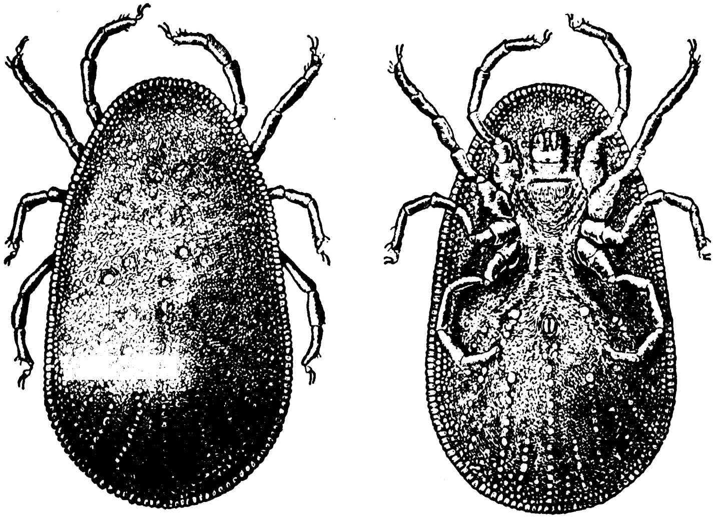


Fig. 13. Argas persicus. Dorsal and ventral views of female. (After Bishopp.)

INTERNAL ANATOMY

The internal anatomy has been studied by a number of investigators. A brief résumé is here presented in order that the student may understand the main structures concerned with digestion, respiration, and reproduction. The

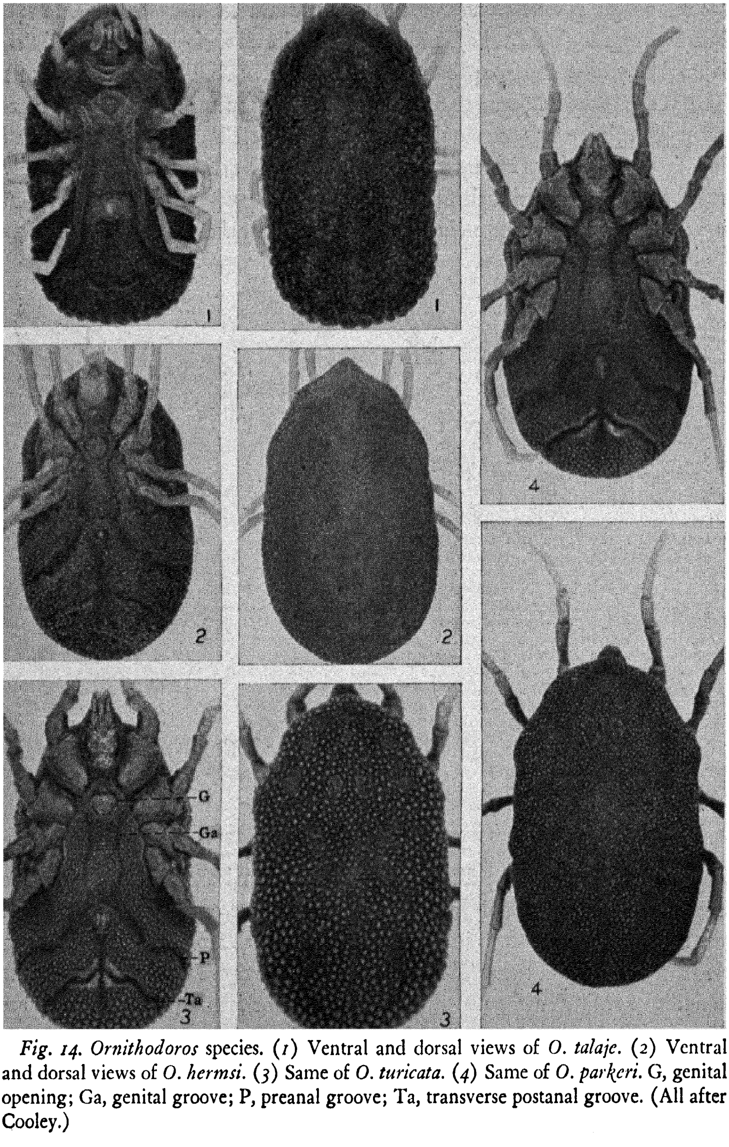
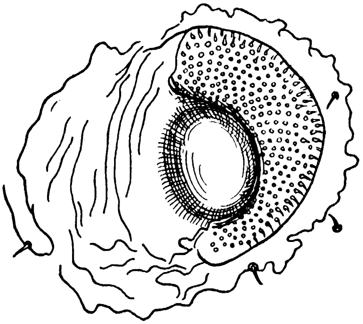


Fig. 14. Ornithodoros species. (*1*) Ventral and dorsal views of *O. talaje.* (*2*) Ventral and dorsal views of *O. hermsi.* (*3*) Same of *O. turicata.* (*4*) Same of *O. parkeri.* G, genital opening; Ga, genital groove; P, preanal groove; Ta, transverse postanal groove. (All after Cooley.)

mouth parts have already been described. It is now necessary to indicate their function and the method of obtaining blood. The tick, placed on its host, proceeds to attach by breaking the skin with the sharp cutting articles situated at the ends of the cheliceral shafts. The articles, controlled by powerful muscles, soon lacerate the tissues, and the hypostome is forced into the wound. The strong recurved teeth of the hypostome are firmly embedded and are forced deeper and deeper as the chelicerae cut the tissues. Soon the entire capitulum, except the palpi, which never enter the wound, are deep in the flesh of the host.



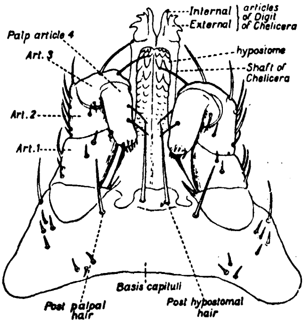


Fig. 15 (left). Argas persicus. Spiracle. (After Nuttall.)
Fig. 16 (right). Capitulum of *Argas persicus.* (After Nuttall.)

Once the tick is attached, the blood is extracted by means of a powerful pumping pharynx (Figs. 7,17). The buccal cavity lies between the palpi within the anterior part of the basis capituli and above the hypostome. It is tubelike and ends posteriorly in a small bayou, widened out laterally, into which open the salivary ducts. The secretion of the salivary glands has been shown, in some cases, to possess an anticoagulin and enables the tick to obtain a steady flow of liquid nourishment. Leading from the floor of the buccal cavity at its posterior end is the short pharynx.

Sen (1935, 1937) describes a peculiar structure ("stylet") overlying the entrance to and at the anterior end of the pharynx. Bertram (1939) apparently refers to the same structure as the tongue, and Arthur (1946) describes it in detail. According to Bertram and Arthur, this structure closes the entrance to the pharynx when the muscles of the pharynx contract to force the blood into the esophagus. It thus prevents the backflow of the blood into the wound.

The pharynx is a chitinous tube richly supplied with dilator and contractor muscles. It terminates in the thin-walled, short esophagus, which passes through the brain and thence to the stomach or mid-intestine. The mid-intestine (Fig. 17 St) consists of a short, thin tube with numerous large diverticula. The diverticula generally arise at the anterior and posterior ends of the mid-intestine. Their number, length, and shape vary in the different species. These diverticula are capable of great distension and enable the ticks to extract a large amount of blood at one feeding. Ticks which drop off their hosts at each feeding are thus furnished with a food supply that enables them to withstand long periods of starvation. The hind intestine arises from the lower surface at the posterior end of the mid-intestine. It appears as a delicate white cord and is supposed to be largely functionless in most ticks. In some, like *Argas persicus,* discharges of wastes take place, but in the great majority of ticks excretion probably occurs through the Malpighian tubules, skin, and other organs. The hind intestine terminates in a saclike rectum. A single Malpighian tubule arises from each side of the rectum. Each tubule is long and winds about and among the internal organs. Each is more or less filled with a whitish substance, which is evacuated through the rectum. These tubules are probably excretory organs.

The salivary glands, two in number, lie in the anterior portion of the body, extending backward on each side to the base of or beyond the third pair of legs (Fig. 17 Sga). Each gland appears like a small bunch of grapes and is composed of rather large secretory cells that pour out their secretions through an independent duct. Each duct opens near the base of the buccal cavity. Another pair of glands that appear to have considerable importance and about which little is known are the coxal glands. These open near the base of the first pair of coxae. They are known to discharge a secretion while or just after feeding (*Argas* and *Ornithodoros*). The exact function of these glands has not yet been determined. It is known, however, that certain spirochetes are transmitted to new hosts by means of the fluid from these glands (e.g., *Ornithodoros moubata* and relapsing fever).

The reproductive system of the female consists of a duplex ovary located just above the posterior end of the mid-intestine. The ovary extends across the body, and each end terminates in an oviduct. The oviduct from each side runs forward as a long coiled tube. The oviducts unite at their anterior ends to form the uterus (Fig. 17). From the uterus the vagina leads to the external orifice (Figs. 5,12). Surrounding the vagina are various glands that are active at the time of egg laying.

The male reproductive system consists of a duplex testis occupying a position similar to that of the ovary in the female. A vas deferens extends forward from each end of the testis. These unite near the external orifice. The sperm

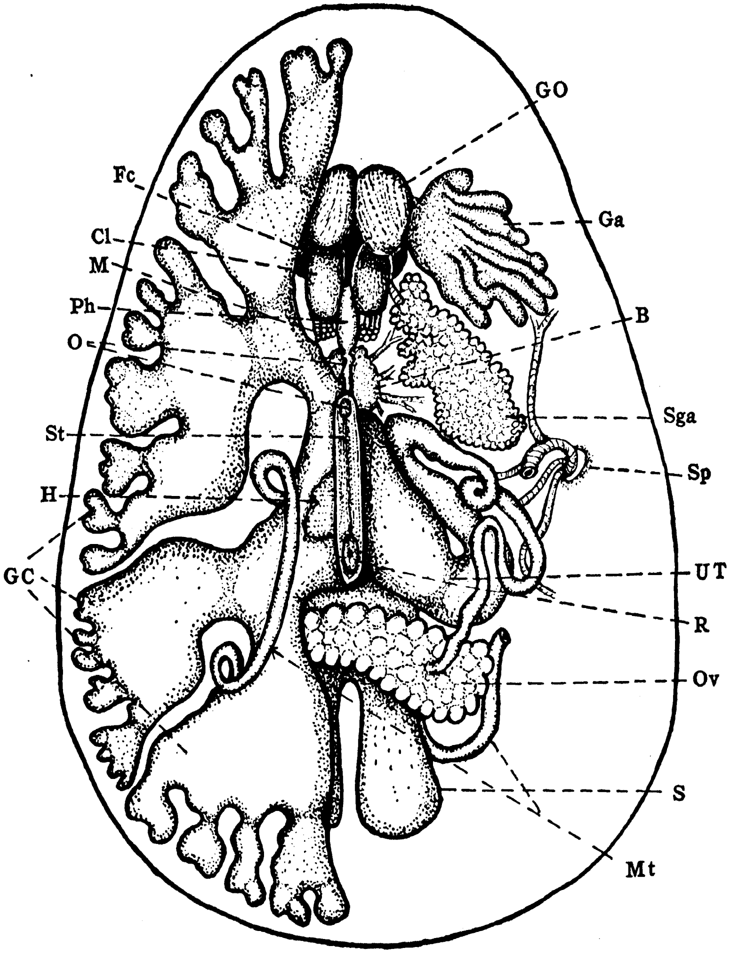


Fig. 17. Argas persicus. Ventral view of dissection of young female. The left side of the figure represents internal organs as they appear after removal of integument; on the right side part of the stomach and intestinal caeca have been removed. B, brain; Cl, chelicera; Fc, occipital foramen; Ga, glandular part of Gené's organ; GC, caeca of gut; GO, Gené's organ; H, heart; M, muscles of chelicera; Mt, Malpighian tubules; O, esophagus; Ov, ovary; Ph, pharynx; R, rectum; S, rectal sac; Sga, salivary gland; Sp, spiracle; St, stomach; UT, uterus. (Adapted from Robinson and Davidson.)

collects in a lobular swelling (seminal vesicle) situated near the junction of the vasa deferentia. Here, in a complicated manner, the spermatozoa are formed into spermatophores.

Another organ that requires description is Gené's organ. It is associated with egg deposition (Fig. 7, Ge). In the Ixodidae it is located directly beneath the scutum and opens to the exterior between the scutum and the basis capituli; in the Argasidae it is just in front of the capitulum. Gené's organ is glandular in structure, is present only in the females, and becomes functional at the time of egg deposition.

The structure of the other internal organs need not concern us here. Full details may be obtained by consulting the references.

SYNOPSIS OF THE IXODOIDEA

The Ixodoidea contains two families, the Argasidae and the Ixodidae. The families may be separated by the following key:

1. Scutum lacking; capitulum ventral, usually concealed beneath the anterior margin, and always subterminal; body alike in both sexes (Fig. 14) . . . . *Argasidae*
2. Scutum present; in the males the scutum extends over the entire dorsal surface; in the females, nymphs, and larvae only on a portion of the anterior dorsal surface; capitulum terminal and always visible from the dorsal surface (Fig. 9) . . . . *Ixodidae*

THE FAMILY ARGASIDAE

The family Argasidae consists of those ticks that lack a scutum, the so-called "soft ticks." There is very little sexual dimorphism, the males closely resembling the females. The capitulum is always inferior, and the spiracles are small and located anterior to coxa IV. In the adults the integument is leathery, wrinkled, granulated, mammillated, or provided with tubercles. The palpi are free and all the segments are freely movable. The porose areas are absent. The adults, even when engorged, never increase greatly in size; when fasting their flattened appearance bears some resemblance to bedbugs. Their principal hosts are birds (especially poultry), domestic animals, rodents, bats, and man. They are found commonly in the habitats of their hosts as in rodent burrows, bat roosts, poultry houses, caves, and human abodes as well as on the ground where they drop from their hosts. They appear to be chiefly nocturnal in their feeding habits. There are only four well-recognized genera: *Argas, Ornithodoros, Antricola,* and *Otobius.*

KEY TO THE GENERA OF ARGASIDAE

1. Margin of the body thin and acute; a sutural line separating the dorsal and ventral surfaces (Fig. 13) . . . . *Argas*
   Margin of the body not thin and acute, but if so no sutural line separating the dorsal and ventral surfaces (Fig. 14) 2
2. Nymphs with the integument beset with spines; hypostome well developed; adults with the integument granular; hypostome vestigial *Otobius*
   Nymphs with the integument not beset with spines; mammillated or tubercular; hypostome not vestigial in either nymphs or adults 3
3. Hypostome scooplike on dorsal surface, broad at base. (Known from bats; only 2 species) . . . . *Antricola*
   Hypostome never scooplike on dorsal surface, not so broad at base. (On various classes of animals including bats and man; a large genus) . . . . *Ornithodoros*

The genus *Argas* Latr. contains only a few species, but some of these are world-wide in distribution. The following key will aid in the identification of the common species:

1. Body nearly circular, discoidal . . . . *vespertilionis* Latr.
   Body not circular, longer than broad 2
2. Margin of body striate 3
   Margin of body not striate, marked off by distinct quadrangular "cell-like" plates (Fig. 13) . . . . *persicus* Oken
3. Body subconical in front; dorsum marked with polygonal depressed areas; large species, 15 by 10 mm. (Known from East Africa) . . *brumpti* Neum.
   Body rounded in front; dorsum marked with fine wrinkles and discs as in *persicus* (species not so large). (Parasitic on pigeons and widely distributed in Europe, North Africa, and northern South America; reported from the U.S.A.) . . . . *reflexus* Fabr.

The genus *Ornithodoros* Koch contains many important species that attack man and act as vectors of serious diseases. They occur in many parts of the world, but none of the species is known to be world-wide in distribution. Nuttall (1908) listed only 11 well-established species, but at present nearly 50 species have been described, though some of them are of doubtful validity.

KEY TO THE MORE COMMON SPECIES OF ORNITHODOROS

1. Cheeks present (flaps at sides of camerostome) 2
   Cheeks absent 5

2. Tarsi with humps (Fig. 12) though they may be small. (From Brazil) .... *brasiliensis* Aragão
   Tarsi without humps 3
3. Tarsus IV with long subapical protuberance .... *tholozani* (Labou. and Mégn.)
   Tarus IV without long subapical protuberance 4
4. Discs large and easily seen. (Southern U.S.A. south to Argentina) (Fig. 14) .... *talaje* Guérin-Mén.
   Discs very small and inconspicuous. (Known only from human abodes; Panama, Colombia, and Venezuela) .... *rudis* Karsch
5. Integument not strongly mammillated, appearing more or less wrinkled; dorsum with discs, two elongate, parallel discs near front being distinctive. (India, Persia, Russian Turkestan, Palestine) .. *lahorensis* Neum.
   Integument strongly mammillated; discs present or absent but lacking the two described above 6
6. Eyes present 7
   Eyes absent 8
7. Anterior eyes much larger than posterior. (Pacific coast of U.S.A., California to Mexico) .... *coriaceus* Koch
   Anterior and posterior eyes about equal in size. (Arabia, Africa, India, Ceylon) .... *savignyi* Aud.
8. Dorsal humps present on all tarsi and prominent (Fig. 12 Dh) 9
   Dorsal humps, when present, not on all the tarsi 10
9. Tarsus IV with three humps. (Hot dry areas of Africa from Lake Chad east and south to Cape Colony) .... *moubata* Murray
   Tarsus IV with one apical hump or the hump might be considered the apical protuberance. (Southern Brazil, Argentina, Paraguay, and Bolivia) .... *rostratus* Aragão
10. Tarsi bifurcate and with dorsal humps. (Algeria) .... *foleyi* Parrot
    Tarsi not bifurcate and without humps on all or some of the tarsi 11
11. Dorsal humps absent from all the tarsi. (Western United States.) (Fig. 14) .... *hermsi* Wheeler, Herms, and Meyer
    Some of the tarsi with dorsal humps 12
12. Dorsal humps on the tarsi very long; tarsus IV with subapical protuberance or hump; mammillae very large and coarse. (Southern Brazil, Argentina, Paraguay, and Bolivia) .... *rostratus* Aragão
    Dorsal humps not so long: mammillae not so large and coarse 13
13. Tarsus IV without dorsal humps but with subapical protuberance. (Mexico) .... *nicollei* Mooser

Tarsus IV without dorsal humps and without subapical protuberance .. 14

14. Mammillae large (Fig. 14), relatively few and not crowded. (Southwestern United States, Florida, Mexico) .... *turicata* Dugès

Mammillae small (Fig. 14), crowded, and numerous. (Western United States) .... *parkeri* Cooley

The genus *Otobius* contains only two North American species. *O. megnini* is the "spinose ear tick" of cattle and horses and has been recorded from man. *O. lagophilus* Cooley and Kohls is reported only from cottontail rabbits and jack rabbits from the western United States and Canada. Both species can be easily recognized as nymphs by their spinose integument. The genus *Antricola* occurs on bats or in bat roosts. Only two species are known, both from the Americas.

THE FAMILY IXODIDAE

The family Ixodidae contains those ticks that have a scutum or shield and have been called the "hard ticks." Sexual dimorphism is marked, the males being completely covered on the dorsum by the scutum and incapable of great distention; the females may become greatly enlarged when engorged, and the scutum appears as a small shield behind the capitulum. The capitulum is always terminal, and, in the females, porose areas are present. This family contains the great majority of ticks and is world-wide in distribution. Their principal hosts are mammals, reptiles, amphibians, and birds. It is not possible to give an adequate key to all the described genera as some of them are rare and not well known or studied.

KEY TO THE PRINCIPAL GENERA OF IXODIDAE

1. Anal groove surrounds the anus in front (Fig. 10); eyes absent. (World-wide in distribution) .... *Ixodes*

Anal groove curves about the anus posteriorly (Fig. 4) or is absent; eyes present or absent 2

2. Eyes absent 3

Eyes present 4

3. Inornate; festoons present; palpi short, conical when closed and segment 2 projects laterally (except in rare cases) beyond the basis capituli (Fig. 9); coxa I never bifid. (Distribution world-wide) ...... *Haemaphysalis*

Ornate; palpi long, segment 2 especially long; festoons present. (Occur mainly on reptiles; tropical and subtropical) .... *Aponomma*

4. Anal groove absent or very indistinct; inornate; eyes present and mar-

ginal; festoons absent; palpi very short, second and third segments compressed and ridged dorsally and laterally; males with adanal and accessory shields. (Tropical and subtropical) .... *Boophilus*

Anal groove present and distinct; ornate or inornate but without all of the above combination of characters 5

5. Ornate; eyes and festoons present; eyes marginal; abdomen without a pair of terminal protrusions capped by sclerotized points 6

Inornate, but if ornate (rarely in *Hyalomma* and *Rhipicephalus*) with a pair of abdominal protrusions capped by sclerotized points 7

6. Palpi short; second palpal segment not twice as long as wide; hypostome with the denticles arranged in 6 rows, 3 on each side (expressed as 3/3) and occupying most of its length. (Distribution world-wide) .... *Dermacentor*

Palpi long; second segment twice as long as wide; hypostome with denticles largely restricted to the apical half and arranged usually 3/4 or 4/4. (Tropical and subtropical) .... *Amblyomma*

7. Eyes not on the margin of scutum but moved inward; if ornate with a pair of abdominal protrusions capped by sclerotized points. (Old World, tropical and subtropical) .... *Hyalomma*

Eyes located on margin of scutum; without the abdominal protrusions .. 8

8. Ventral plates or shields absent in both sexes 9

Ventral plates or shields present in the males, absent in the females; basis capituli usually hexagonal in dorsal view. (Distribution world-wide) .. .. *Rhipicephalus*

9. Basis capituli rectangular in dorsal view; coxae not increasing greatly in size from I to IV; coxa IV without spines; spiracles subcircular. (Tropical America) .... *Otocentor*

Basis capituli hexagonal in dorsal view; coxae increasing greatly in size from I to IV; coxa IV with very long spines; spiracle comma-shaped. (Africa) .... *Rhipicentor*

Over three hundred species of ixodid ticks have been described. It is not possible to give keys to the species included in the different genera. In the bibliography will be found references in which keys to the species of certain genera are given. These references are indicated by a dagger. The genus *Dermacentor* contains species important as transmitters of human diseases, and the following key will aid in recognizing the North American species.

KEY TO THE IMPORTANT AMERICAN SPECIES
DERMACENTOR

1. Spurs on coxa I diverging from their base outwards. (Southwestern U. Texas to Oregon; hosts mainly rabbits) .... *parumapertus* Neum.
   Spurs on coxa I with proximal edges closely parallel or slightly diverging near apices 2
2. Spiracular plate oval, without dorsal prolongation and with goblets few and large. (Widespread in North America) .... *albipictus* Pack.
   Spiracular plate oval, with dorsal prolongation and the goblets numerous or moderate in numbers 3
3. Cornua long, especially so in the males. (West coast from Oregon to southern California) .... *occidentalis* Marx
   Cornua short or of moderate length 4
4. Goblets of spiracular plate very small and numerous. (Eastern North America to Saskatchewan south through central Texas) .. *variabilis* Say
   Goblets of spiracular plate large and not so numerous or densely packed. (Western North America, Saskatchewan to British Columbia south to northern New Mexico) .... *andersoni* Stiles

BIOLOGY OF TICKS

Ticks are all external parasites of mammals, birds, reptiles, and some amphibia. During their life cycles they pass through four stages—egg, larva, nymph, and adult. All species oviposit on the ground or in the habitats of their hosts, usually in sheltered places (Fig. 18). The time required for the development of the embryo within the egg varies widely not only with the species but also with temperature, moisture, and other climatic factors. The hexapod larva (Fig. 19), which hatches from the egg, is very active (there are a few known exceptions) and seeks out its host in various ways. After feeding, the larva drops off and molts on the ground or remains on its host and molts. The nymph, the next stage, possesses eight legs, and the tracheal system with its spiracles (lacking in the larva) are now present. The external opening of the genital organs is still lacking. After another feeding the nymph again leaves its host and molts, or it may remain and molt on the host. This is the adult stage, which is usually quite similar to that of the nymph except that the external genital orifice is present. In the Argasidae there may be several nymphal stages, but all ticks of the family Ixodidae have, as far as known, only a single nymphal stage. The adults are not known to molt but feed and

r hosts or on the ground. Shortly after mating the [redacted]
. In the Ixodidae the males usually die shortly after mating
, after laying their batches of eggs. In the Argasidae the adults are
-lived, the males and females living for a long time, even several years.
gg laying usually takes place after each blood meal.

Though the above statement represents the general life cycle of ticks, each species undergoes its own peculiar developmental cycle. Some ticks complete their life cycle on a single host, molting and mating without leaving the host; such ticks are known as one-host ticks, as *Boophilus annulatus* and *Dermacentor albipictus;* some require two hosts, as *Rhipicephalus evertsi* and *Hyalomma aegyptium,* and are called two-host ticks; many others require three hosts, dropping off after each feeding, and are known as three-host ticks, as *Dermacentor andersoni, D. variabilis,* and many other species; and still other ticks require even more hosts, as many of the argasid ticks such as *Argas persicus, Ornithodoros moubata,* and *O. savignyi,* and may be called many-host ticks. The relation of ticks to their hosts is shown graphically in Fig. 20, and nearly all the known types of life cycles are indicated.

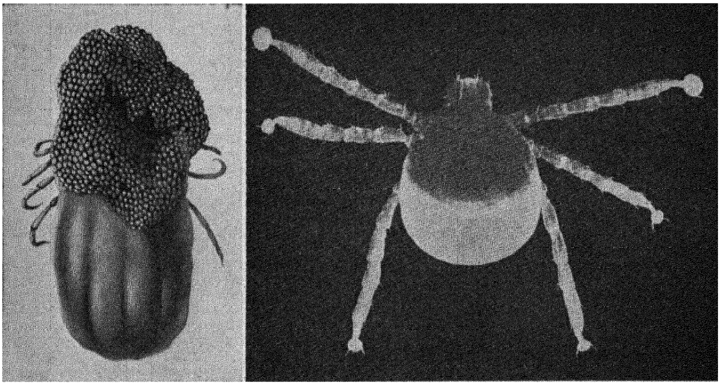


Fig. 18 (*left*). *Dermacentor albipictus.* Female laying eggs. (After Department of Agriculture, Division of Entomology, Canada.)

Fig. 19 (*right*). *Boophilus annulatus.* Recently hatched larva. (After Cotton.)

Sexual reproduction occurs generally in ticks, though Aragão (1912, 1936) and Brumpt (1924) have shown that *Amblyomma rotundatum* (*agamun*) probably reproduces normally parthenogenetically. Mating takes place, in most cases, on the host, the male seeking out the female. In all species so far described, the male attaches beneath the female and uses his mouth parts as an

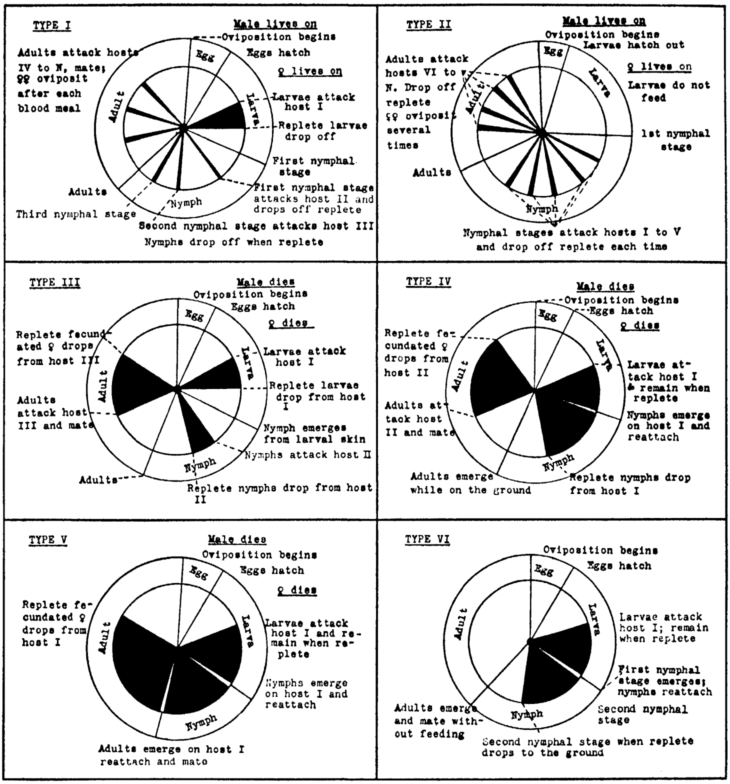

TYPE I
Male lives on
Oviposition begins
Eggs hatch
♀ lives on
Adults attack hosts IV to N, mate; ♀♀ oviposit after each blood meal
Egg
Larva
Adult
Larvae attack host I
Replete larvae drop off
First nymphal stage
First nymphal stage attacks host II and drops off replete
Adults
Nymph
Third nymphal stage
Second nymphal stage attacks host III
Nymphs drop off when replete
TYPE II
Male lives on
Oviposition begins
Larvae hatch out
♀ lives on
Adults attack hosts VI to N. Drop off replete ♀♀ oviposit several times
Egg
Larva
Adult
Larvae do not feed
1st nymphal stage
Adults
Nymph
Nymphal stages attack hosts I to V and drop off replete each time
TYPE III
Male dies
Oviposition begins
Eggs hatch
♀ dies
Replete fecundated ♀ drops from host III
Egg
Larva
Adult
Larvae attack host I
Replete larvae drop from host I
Adults attack host III and mate
Nymph emerges from larval skin
Nymphs attack host II
Adults
Nymph
Replete nymphs drop from host II
TYPE IV
Male dies
Oviposition begins
Eggs hatch
♀ dies
Replete fecundated ♀ drops from host II
Egg
Larva
Adult
Larvae attack host I & remain when replete
Adults attack host II and mate
Nymphs emerge on host I and reattach
Nymph
Adults emerge while on the ground
Replete nymphs drop from host I
TYPE V
Male dies
Oviposition begins
Eggs hatch
♀ dies
Replete fecundated ♀ drops from host I
Egg
Larva
Adult
Larvae attack host I and remain when replete
Nymphs emerge on host I and reattach
Nymph
Adults emerge on host I reattach and mate
TYPE VI
Oviposition begins
Eggs hatch
Egg
Larva
Adult
Larvae attack host I; remain when replete
First nymphal stage emerges; nymphs reattach
Second nymphal stage
Adults emerge and mate without feeding
Nymph
Second nymphal stage when replete drops to the ground

Fig. 20. Life cycles of ticks. The black areas (sectors) represent the periods of blood taking. Type I: *Argas persicus, Argas reflexus* (?), *Ornithodoros* sp. Type II: *Ornithodoros moubata, O. savignyi.* Type III: *Ixodes ricinus, I. hexagonus, I. canisuga, Dermacentor reticulatus, D. occidentalis, D. variabilis, D. andersoni, Haemaphysalis leachi, H. punctata, H. leporis-palustris, Amblyomma hebraeum, A. maculatum, A. cajennense, A. americanum, Rhipicephalus appendiculatus, R. sanguineus, R. simus.* Type IV: *Rhipicephalus evertsi, Hyalomma aegyptium.* Type V: *Boophilus annulatus, B. dugesii, Dermacentor albipictus.* Type VI: *Otobius megnini.* (There are other types of life cycles not shown on the chart.)

external genital organ. After the male has distended the vulva of the female with his mouth parts, he moves forward until his genital orifice is directly over that of the female. Then with great rapidity a viscid spermatophore is applied to the vulva and is promptly received by the female. The females may mate several times with different males.

Egg deposition in ticks is a rather remarkable performance. The eggs are always found in front of the female (Fig. 18), whereas the genital opening is on the ventral surface (Fig. 5). The transfer of the eggs is accomplished in the following manner: When ready to oviposit the female withdraws the capitulum as far as possible within her body and Gené's organ is extruded. The vulva is partially everted, and an egg is protruded and rolled around until it comes in contact with the sticky Gené's organ; when this is done the organ is withdrawn, and the egg is carried to the dorsal surface and pushed off in front of the tick. This process is repeated for each egg. That it must be a laborious procedure is evident when it is remembered that some ticks lay as many as 12,000 eggs. The secretion of Gené's organ is believed to be protective.

Many ticks are known to be long-lived and to be able to withstand long periods of starvation. Various larvae are known to live seven or eight months or even longer without any food; adults of *Ornithodoros moubata* have survived without food for over a year; *O. savignyi* for over two years; *O. hermsi* for four years; *Argas persicus* for three or four years; *A. reflexus* for five years; *Dermacentor andersoni* at least four years. Many other species of ticks have been kept alive without food for varying lengths of time. Ruttledge (1930) kept a female of *Argas brumpti* (collected in the wild) alive for nearly 12 years; Francis (1938) kept *Ornithodoros turicata* alive for five years unfed and infected with spirochetes of relapsing fever; another group he kept alive unfed for four years, and then they infected a monkey with relapsing fever; two and a half years later the same group fed on a monkey and infected it with relapsing fever, demonstrating six and a half years of natural infection. In 1942 Francis records the maximum length of life of this tick under experimental conditions as 9 years 10 months and 7 days.

SPECIAL BIOLOGIES

Owing to the importance of ticks as vectors of human and animal diseases a few of the life histories of the more important species need to be given in some detail.

THE FAMILY ARGASIDAE

THE GENUS *ARGAS*: *Argas persicus* (Oken) is the common fowl tick (Fig. 13). The males and females appear very similar but may be separated by the shape of the genital opening. In the males the genital opening appears crescent-shaped, whereas in the females it is a narrow transverse slit. The mature female, unengorged, measures from 5 to 8 mm. in length and the male from 4.5 to 6 mm. The domestic fowl is the principal host, though turkeys, geese, and ducks are attacked; wild birds are also frequent hosts, and man is occasionally attacked when associated with poultry.

The fowl tick has a world-wide distribution and occurs in the warm and dry regions of Europe, Asia, Africa, the Americas, and Australia. The distribution in North America is shown in Fig. 21. In our warm poultry houses it frequently occurs far north of its range, as in Baltimore, Maryland.

The mature males and females feed at night and become engorged in less than an hour. Dropping from their hosts they seek shelter in any convenient hiding place. The females deposit a batch of eggs after each blood meal, and each female may lay several batches of eggs. Over 600 eggs are laid by the average female. The eggs hatch in from 10 days to several weeks. The larvae attach to their hosts and become engorged in about 5 days. They drop from their hosts and molt to the first nymphal stage in about a week. The first-stage nymph now feeds at night, and a second molt takes place in about another week. Another molt occurs about a week later, and the third-stage nymph after feeding usually molts to the adult. The entire life cycle from egg to adult may be completed in about 30 to 40 days if food and warmth are suitable. This tick is a serious pest of poultry, killing young birds in large numbers. It is the vector of a serious disease of fowls, spirochetosis, caused by *Spirochaeta gallinarum* Blanchard (*S. marchouxi* Nuttall). Recently (1943) it has been reported capable of transmitting anaplasmosis of cattle. It or a closely allied species, *Argas mianensis,* is said to attack man commonly in Persia and produces a fever known as Mianeh fever.

Argas reflexus (Fabr.) is primarily a parasite of pigeons and occurs most commonly in the Old World. It also occurs in northern South America, and Cooley (1944) records a few localities in the United States. Why it has not spread among pigeons in this country is not known. *A. brumpti* Neum. is our largest known argasid tick, measuring nearly 20 mm. in length. It has been taken only in East Africa (Somaliland, Kenya, and the Sudan). *A. vespertilionis* (Latr.) is a beautiful nearly circular tick; it is recorded from bats in England, Europe, North Africa, South Africa, southern India, and Australia. Patton and Cragg reared this species on bats in India; it completes its life cycle in about two months.

THE GENUS *ORNITHODOROS:* Many species of this genus are important agents in the transmission and dissemination of human diseases. Only a few of the species can be discussed here.

Ornithodoros moubata (Murray), the eyeless tampan, is probably the best known tick (Fig. 12) that prefers man as its host in all stages. It also feeds on pigs, goats, dogs, sheep, and other domesticated animals. It is found only in Africa, where it is widely distributed in the hot dry areas from Lake Chad eastward to the Red Sea and south to the Cape Province. It is also reported from northwestern Madagascar. Here they are found most commonly in the rest houses along the caravan routes, in native huts, and in the village houses. The ticks prefer the dry places such as about hearths and bed platforms, in the cracks and crevices of the mud floors, in the dry grass walls, and about the doorsills. The females lay their eggs in batches at night, placing them in cracks and crevices or in hollows made in the ground. Each female normally lays several batches of eggs, a batch after each blood meal. Jobling (1925) records each female as laying from 600 to over 1200 eggs. The eggs hatch in from eight days to two or three weeks. The larvae, however, do not leave the eggs but remain within the shells and molt to the nymphal stage in about four days. According to Jobling, the males undergo four molts and the females five molts before reaching maturity. Both the nymphs and adults are nocturnal and feed primarily at night. The nymphs require about a half-hour to become engorged and then drop from their hosts. The adults are long-lived and can live for several years. This tick is the important vector of African relapsing fever throughout its range.

Ornithodoros savignyi (Aud.), the eyed tampan, closely resembles *O. moubata* but is easily distinguished by the possession of two pairs of eyes, all about the same size. The life history of this tick is very similar to that of *O. moubata.* The females oviposit after each blood meal, and the total number of eggs varies widely. Cunliffe (1922) reports a total of 400 under laboratory conditions. Under experimental conditions the life cycle from egg to adult varied from 60 to over 103 days. Its hosts are various domestic animals as horses, cattle, camels, dogs, pigs, goats, but it seems to prefer man (Bedford, 1934). Its distribution in Africa closely corresponds to that of *O. moubata,* and in addition it is found in parts of Arabia and India. Senevet (1937) reports it from Tunisia, Algeria, and North Africa generally. It is known to be a vector of relapsing fever.

Ornithodoros hermsi Wheeler, Herms, and Myer is a comparatively small tick (Fig. 14), not much more than half the size of *O. turicata.* It may be recognized by the size and the absence of dorsal humps on tarsus I. It has been taken only at high elevations (3000 to 9000 feet) in the mountainous regions of the western United States (California, Colorado, Oregon, Washington, Nevada, and Idaho). The tick is primarily a parasite of small mammals, as the western chipmunks, *Eutamias* spp., and probably other rodents. It has been taken in the nests of its hosts, and Davis (1939) reports taking many ticks in chipmunks' nests in old Douglas fir (*Pseudotsuga taxifolia*) stumps in eastern Colorado at an elevation of 8800 feet. Wheeler (1943) gives a full account of the biology of this tick. The females deposit their eggs in batches, the maximum number obtained being 232. The eggs hatch in 9 to 24 days (under constant temperature of 75° F. and 90 per cent humidity); there may be two larval stages and three or four nymphal stages. The normal time for development from the egg to the adult stage is about four and one-half months. The adults are apparently long-lived, as Wheeler kept some females for over four years without any food, and others by occasional feedings for more than six and one-half years. This tick is known to be a vector of relapsing fever in many parts of its range.

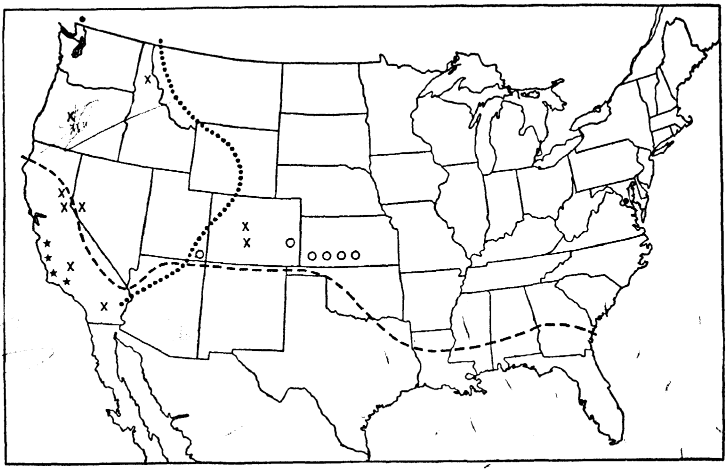


Fig. 21. Distribution of argasid ticks in the United States. *A. persicus,* generally south of the line of dashes, and two isolated spots, one in British Columbia, and one in Baltimore, Md.; *Ornithodoros turicata,* generally south of line of dashes and north indicated by circles; *O. parkeri,* generally west of line of dots; *O. hermsi,* places collected indicated by X's; *O. coriaceus,* indicated by stars. (After Cooley and others.)

Ornithodoros turicata (Dugès) is a large tick (Fig. 14) and is widely distributed in the southwestern United States (Fig. 21), Florida, and parts of central Mexico. It is frequently found in great numbers in caves, in holes of burrowing animals, and in camps. Its hosts include nearly all our domestic animals, rodents, snakes, and terrapins as well as man. Hoffman (1930) reports them as abundant in pigsties in central Mexico. Under experimental conditions Francis (1938) reared the tick from egg to adult in nine months and ten days. He found four nymphal stages, though five nymphal stages were observed in four females and only three nymphal stages in one male. The species is an excellent vector of relapsing fever, and Davis (1943) has demonstrated transovarial transmission to the fifth generation, securing a 100 per cent infection with the fifth generation. He concludes that this tick may be a more efficient "spirochaetal reservoir" than the rodent hosts. Francis (1938) obtained transmission of relapsing fever in infected ticks after four years of starvation; two and a half years later he demonstrated the presence of the spirochetes in ticks that had only one feeding during that period (six and a half years).

Ornithodoros parkeri Cooley (Fig. 14) is very similar to *O. turicata* but may be recognized by the much smaller mammillae. It has been taken in widely separated areas in nine western states from Washington south to southern California and east to Colorado (Fig. 21). Jellison (1940) took large numbers in the nests of the burrowing owl, *Speotyto cunicularia,* and found the larvae of this tick engorged. Its principal hosts are recorded as *Citellus* spp., *Cynomys* spp., *Marmota* sp., *Peromyscus* sp., *Lepus* sp., *Sylvilagus* sp., *Mustela* sp., and man (Cooley, 1944). Davis (1941) reared large numbers of this tick and records two nymphal stages for some males and three to four nymphal stages for females and males. The average developmental time from larval feeding varied from about 53 days to over 250 days. This tick is an efficient vector of relapsing fever, and Davis (1943) has shown experimentally that it can transmit, in all stages, the spotted fevers of the United States, Colombia, and Brazil with equal facility even to the second and fourth generation through the egg. He suggests that this tick may serve as a "spotted fever reservoir" in nature and may occasionally infect man. The tick is apparently long-lived as Davis has kept nymphs and adults for four years without feeding.

Ornithodoros talaje (Guérin-Mén.) occurs from California and Kansas south to Argentina. In the tropics and subtropics of the Americas it is cosmopolitan and is frequently present in large numbers. In the United States it is recorded from California, Nevada, Arizona, Kansas, Texas, and Florida. This tick (Fig. 14) has been confused with *O. rudis* Karsch and *O. kellyi* Cooley and Kohls, and it is difficult to interpret the published accounts. Its hosts are known to be various mammals, birds, and reptiles. The larval stage is most common on rats in Panama, and in the United States this tick has been taken in association with rodents. Dunn (1931, 1933) reports it in houses attacking man, and the later stages were found in beds and other parts of the homes. The larva of this species requires a long time to feed (several days) and then leaves the host and molts twice before feeding again. There are three to four nymphal stages, but the nymphs require only a few hours to feed. Under laboratory conditions Davis (1942) has reared this species in eight months. The principal hosts of the larvae are various species of rats, though Dunn has taken them on chickens, opossums, monkeys, cats, and dogs in Panama. This tick is known to be a transmitter of relapsing fever in Panama, Colombia, and Guatemala; relapsing fever spirochetes have been recovered from ticks captured in Arizona and Texas.

Ornithodoros kelleyi Cooley and Kohls is noted here because it has been confused with *O. talaje*. As far as known, this is a parasite of bats, and it has been reported under the name *talaje* from houses in New York, Wisconsin, and Minnesota (Matheson, 1931; Herrick, 1935; and Riley, 1935). It apparently occurs in places where bats live or roost. It also has been reported from houses in Illinois, Iowa, and Pennsylvania (Cooley, 1944). In one house in New York it has been present since 1925, the last tick being found about December 13, 1940.

Ornithodoros rudis Karsch (*O. venezuelensis* Brumpt; *O. migonei* Brumpt) is closely allied to *O. talaje,* and these two species have been confused in literature. However, man is the only known host of *O. rudis,* which is a house dweller, often occurring in large numbers in primitive dwellings where it hides during the day in cracks, crevices, holes, bedding, and similar places. It is a night feeder. The larvae feed rapidly and molt after feeding; there are two to four nymphal molts. Under experimental conditions the life cycle from egg to adult may occupy only three months (Davis, 1942). Its known distribution is Panama, Colombia, Venezuela, and Paraguay. It is the important transmitter of relapsing fever in Panama, Colombia, and Venezuela. Davis (1943) has shown that the causative agents of the spotted fevers of Colombia, of Brazil, and of the United States can be conserved in the tissues of this tick for 343 days, 191 days, and 243 days, respectively; furthermore, the Colombian spotted-fever agent was transmitted through the egg to the next generation. Davis did not get transmission by the bites of this tick.

Ornithodoros coriaceus Koch, the pjaroello, is a large tick and is much feared on account of its bite. It occurs in many parts of California extending from near San Francisco south along the coast (Fig. 21) in the more mountainous regions into Mexico, where Hoffman (1930) records it as native to the hot and temperate regions along the Pacific coast to Chiapas. Herms (1939) found it commonly in deer beds among the low scrub oaks. It is a parasite of large mammals and bites man freely. Herms (1916) gives its life history, under experimental conditions, as requiring about 15 months from egg to egg. He also reared mature males in about four months. The larvae require several days (8 or more) to engorge, and then undergo two molts before feeding again. There are three to six nymphal stages. The nymphs and adults feed very rapidly, becoming engorged in 10 to 40 minutes. The females lay several batches of eggs and may live for several years. The bite of this tick is very severe. It is not known to transmit any disease.

A goodly number of other species of *Ornithodoros* have been recorded as biting man and some of them as playing a part in the transmission of disease. *O. brasiliensis* Aragão is reported from Brazil and bites man but is not known to transmit disease. *O. rostratus* Aragão occurs in Argentina, Paraguay, Brazil, and Bolivia. It is said to occur in houses and its bite is severe. *O. nicollei* Mooser was described from Mexico, where it occurs in native huts; Davis (1943) gives its life history, reports it readily infected with the rickettsiae of the spotted fevers of the United States, Colombia, and Brazil, and has proved transovarial transmission. The tick has been taken from dogs, species of *Neotoma,* man, and a rattlesnake. *O. delanoei* Rouhaud and Colas-Belcour was described from porcupine burrows in Morocco. It is a large species, the female being 18 mm. in length. The same authors (1936) give an account of its life history, concluding that it requires about five or six years from egg to maturity (under experimental conditions). *O. erraticus* (Lucas) [*O. marocanus* Velu] occurs throughout the western littoral of the Mediterranean and south to Senegal. Brumpt (1936) records this tick as infected with *Spirochaeta duttoni* at Dakar; it is a vector of relapsing fever in Spain and parts of North Africa. It is found commonly in pigsties and burrows of various animals such as porcupines, jackals, and rats. *O. foleyi* Parrot was described from Algeria and reported as feeding on man. *O. tholozani* (Laboulbene and Mégnin) [= *O. papillipes* Birula] is reported from the Caucasus, Turkestan, Iran, Syria, Palestine, and the island of Cyprus. It is known to transmit relapsing fever in Russia and Cyprus. Russian workers report it as living at least 25 years. Its hosts are camels, chickens, porcupines, jerboas, and various rodents. It readily feeds on man and is found in human dwellings. *O. lahorensis* Neum. is widely distributed in Russian Turkestan, Iran, Transcaucasia, Tibet, Palestine, Asia Minor, and Cyrenaica; it is also found in India (the Punjab). It is not known to transmit relapsing fever but transmits anaplasmosis of sheep. Its bite is severe and is recorded as killing sheep. *O. normandi* Larrousse is reported as abundant near El Kef, Tunisia; it bites man readily.

THE GENUS *OTOBIUS:* This genus has, at present, only two well-defined species. *O. megnini* (Dugès), more generally known as *Ornithodoros megnini,* is the spinose ear tick. It lives in the ears of its hosts, which are mainly horses and cattle. It also attaches to the ears of mules, asses, sheep, goats, hogs, dogs, cats, coyotes, deer, rabbits, and some other animals. It receives its name from the spiny last nymphal stage, which is the stage most commonly seen in the ears of its host. This stage leaves the host and molts on the ground into a smooth, typical tick; however, the large hypostome of the nymph is replaced by a vestigial one. The adult does not feed. The female lays her eggs on the ground, and the larvae on hatching are very active. Reaching the ears of their hosts, they attach deep down in the folds and become fully engorged in about a week. Then follows the larval molt; there is a second molt soon after, and this is the last nymphal stage, the spinose stage. The entire life cycle may be completed in a month and a half under favorable conditions, or it may be greatly prolonged. The adults may survive for a year or more. This tick was originally described from Mexico but has become widely distributed throughout many parts of the world. In North America it extends from British Columbia south and east to Kentucky and North Carolina. I have taken this species in the ears of cattle shipped from Texas to Ithaca, New York. The species is widespread in Mexico and parts of South America. Brumpt (1936) states that it is well established in the Transvaal and other parts of South Africa. Kingston (1936) reports it in the ear of a gelding that had been born and reared in Australia. This tick has been reported found several times in the ears of man.

Recently Cooley and Kohls (1940) described another species, *O. lagophilus,* from rabbits. The species occurs in the northwestern United States and British Columbia.

In addition to the species mentioned above many others are known. The genus *Ornithodoros* contains several species described from bats, bat roosts, or bat dung, as well as from other hosts.

THE FAMILY IXODIDAE

This family contains the vast majority of ticks distributed among some 10 or 12 genera. Only a few of the more important species can be treated here.

THE GENUS *BOOPHILUS*: *Boophilus annulatus* (Say) (Figs. 22,23) is the common cattle tick of North America and Mexico. In the United States it is normally restricted to south of 37° North latitude, and in this area the tick has been largely eliminated by dipping and other practices; where present it is under strict quarantine control. The tick is a one-host tick. The females deposit their eggs on the ground, each female laying from 3000 to over 5000 eggs. The incubation period of the eggs depends largely on temperature and moisture and varies from 19 days (minimum) in summer to 180 or more days in late autumn, with varying periods between these extremes during the rest of the year (Graybill, 1941). The seed ticks are very active and climb up blades of grass and various objects to await a passing host. The larvae can survive long periods—from a maximum of 85 days for eggs hatching in July to 234 days for eggs hatching in October. The developmental period on the host (larva, nymph, adult) varies from 20 to 65 days. Mating takes place on the host, and the female after engorging drops off; egg laying begins in from three days to as long as nearly 100 days (females dropping in November). This tick is a very important species as it transmits the organism (*Piroplasma bigemina*) of the so-called Texas fever, red-water fever, or hemoglobinuria.

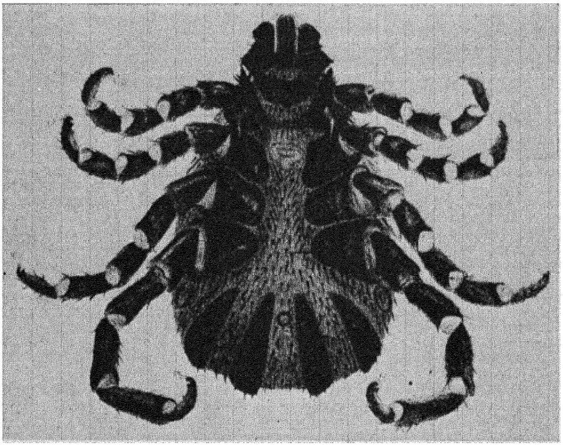


Fig. 22. The cattle tick (*Boophilus annulatus*). Male, ventral view. (After Salmon and Stiles.)

This was demonstrated by Smith and Kilbourne (1893), and they showed that the organism develops in the red blood cells of cattle, destroying them. The tick in feeding obtains the infective stage of this parasite, which undergoes a developmental cycle (later elucidated by Dennis, 1932) and is passed on to the young of the tick through the egg (the so-called transovarial or hereditary transmission). It is of interest to note that this was the first tick that was shown to be an intermediate host of a protozoan parasite and the first case of proven transovarial transmission of any parasite. The principal hosts of this tick, besides cattle, are horses, mules, sheep, goats, and probably deer.

A number of species or subspecies of this tick have been described from various parts of the world: *Boophilus australis* Fuller from Australia, the Philippine Islands, the Dutch East Indies, India, and South America; *B. microplus* Canestrini from South America, Central America, West Indies, Mexico, Florida and probably other parts of the world; *B. decoloratus* Koch from South Africa. Minning (1934, 1936) has added a number of doubtful species.

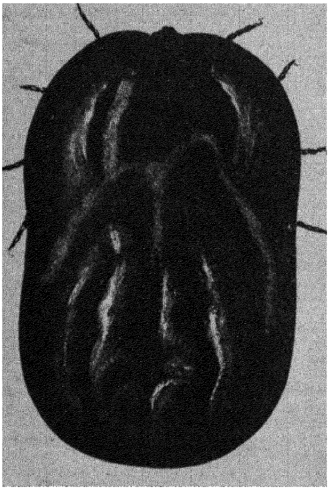
THE GENUS *DERMACENTOR:* This genus contains some very important North American species. The principal characters that readily distinguish this genus are as follows: ornate, with eyes and festoons (always 11); basis capitulum quadrangular in dorsal view; coxae I to IV gradually increasing in size, with coxa IV very large; coxa I always bifid; anal groove posterior; males without ventral shields.

In North America Cooley (1938) describes seven species, and probably over twenty species are at present known from the world. No species are known from South America (Cooley, 1938).

Dermacentor variabilis (Say), the dog tick (Fig. 9) or wood tick, is widely distributed in North America east of a line drawn from eastern Montana south to Texas; it also occurs in Canada east of Saskatchewan; another area is in California west of the Cascade and Sierra Nevada Mountains (Fig. 24). It is most abundant along the Atlantic seaboard from Massachusetts south to Florida and in certain inland areas such as southern Iowa and parts of Wisconsin and Minnesota (Bishopp and Smith, 1938). This is a three-host tick. The adults prefer large mammals such as dogs (the preferred host), cattle, horses, hogs, sheep, man, and a wide variety of wild animals. The adults require from 5 to 14 days to engorge. Mating takes place on the host. Dropping from the host the females lay their eggs in some secluded place on the ground; each female lays from 4000 to 6500 eggs. The eggs hatch in from 26 to 40 days (depending on the temperature), and the larvae can survive without food for at least 11 months. The principal larval hosts are mice (*Peromyscus, Microtus,* and *Pitymys* spp.), and the time of attachment varies from 2 to 14 days. The larvae then drop from their hosts and molt to the nymphal stage. Nymphs can survive at least six months without food. The nymphs attach to the same host as the larvae and engorge in from 3 to 10 days. Dropping from the hosts, the nymphs molt to the adult stage in from three weeks to a much longer period. The entire life cycle from egg to adult varies from 54 days to much longer, depending on the available food supply and the temperature. This tick is the important vector of Rocky Mountain spotted fever and tularemia in parts of its range.

Dermacentor andersoni Stiles (*venustus* Banks) is commonly called the "Rocky Mountain spotted-fever tick" (Figs. 4,5) as it was first shown to be the vector of a peculiar disease of man called "Rocky Mountain spotted fever."

Its distribution is restricted to parts of the western United States and western Canada (Fig. 24). Its greatest abundance is in the northern part of the Rocky Mountain region of the United States, and there it is most common in areas "where the predominating vegetation is low, brushy and more or less open, i.e., in areas where there is good protection for the small mammalian hosts of the larvae and nymphs and sufficient forage to attract the large hosts, either wild or domestic, of the adult ticks. It is relatively quite scarce in heavily timbered areas or country of a strictly grassland, prairie type" (Parker *et al.,* 1937). At present it is known from 14 western states—Washington, Oregon, California, Nevada, Arizona (northern part), New Mexico (northern edge), Utah, Colorado, Idaho, Wyoming, Montana, and the western edge of North and South Dakota and Nebraska; it is also present in southern British Columbia (dry regions of the Kootenay district and north), southern Alberta, and southern Saskatchewan. The tick has been spreading, and it may eventually occupy a much wider range where suitable hosts and conditions exist.



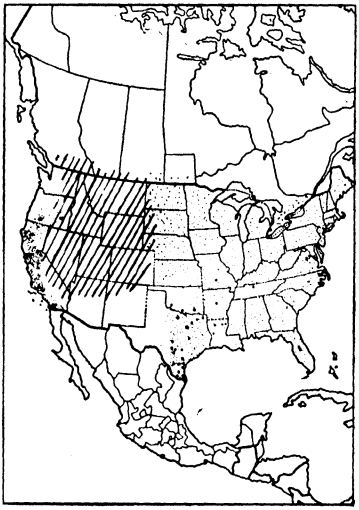


Fig. 23 (*left*). The cattle tick (*Boophilus annulatus*). Fully gorged female. (After Salmon and Stiles.)

Fig. 24 (*right*). General distribution of *Dermacentor variabilis* (dotted area) and *D. andersoni* (lined area) in North America.

This tick is a three-host tick, and its life cycle is interesting and complicated.

The fertilized females drop from the larger hosts during April, May, and June or early July. They deposit their eggs in some protected place on the ground, each female laying from 2000 to 8000 eggs over a period of about a month. The eggs, depending on temperature and other factors, hatch in from one to two months. The larvae attach to some of the smaller mammals, particular rodents, as the ground squirrel (*Citellus columbianus*), pine squirrel (*Sciurus hudsonicus richardsoni*), chipmunks (*Eutamias* spp.), and most of the other native rodents as porcupines, prairie dogs, and various species of rabbits. As Cooley remarks, "Almost any mammal that is available is used." The larvae become engorged in two to eight days and drop from their hosts. Molting takes place on the ground, and the nymphs normally pass the winter unfed. During the following spring and summer the nymphs attach to the same type of hosts as those of the larvae. After engorgement the nymphs drop from their hosts, molt on the ground, and pass the second winter as unfed adults. The following season the adults attach to the larger mammals, preferring horses, cattle, sheep, bears, coyotes, mountain goats, deer, man, and also the jack rabbits, snowshoe rabbits, and porcupines, but usually not any of the smaller rodents. The presence of the larger mammals seems essential for the maintenance of this tick in abundance. They attach from March to July each year and mate on the hosts. The complete cycle from egg to egg thus requires two years, though there are many variations due to the failure to find suitable hosts, climatic factors, and other conditions. The most striking features of the life cycle are its length, two years, and the change of hosts—from small rodents, as larvae and nymphs to the larger mammals as adults. This tick is a very important vector of Rocky Mountain spotted fever, tularemia, "Q" fever, and Colorado tick fever; it is the cause of tick paralysis.

Dermacentor occidentalis Marx can be recognized by the long cornua and, at present, its restricted distribution. It is known only from the Pacific coast along the Coastal Ranges and Cascade Range from northern Oregon to southern California. Cooley (1938) reports it as very abundant in southern Oregon. This is a three-host tick. The adults attach to cattle, horses, deer, dogs, mules, asses, and man. The larvae and nymphs attach mostly to the smaller rodents, such as ground squirrels, wood rats, chipmunks, and rabbits, and occasionally to larger animals. The larvae, nymphs and adults engorge on their hosts in three to six or more days, and the entire life cycle may be completed in less than three months. In nature this tick may be found at all seasons. It is a serious pest of cattle. It also readily attaches to man and its bite is severe. At present it is known to transmit tularemia and it is strongly suspected of transmitting Rocky Mountain spotted fever. Experimentally it can transmit spotted fever in all stages, from stage to stage, and through the egg to the larvae.

Dermacentor parumapertus Neum. is primarily a rabbit tick, as rabbits (all species) are the hosts of all stages. It is rarely found on other hosts. The species occurs in the southwestern United States, from Oregon, southern Idaho, and southern Wyoming south to Mexico and east to Kansas and central Texas. Parker *et al.* (1937) have shown stage-to-stage survival of Rocky Mountain spotted fever in this tick, and it seems probable that the tick may serve as an agent in maintaining the virus in nature in rabbits.

Dermacentor albipictus (Pack.), the moose or elk tick, is markedly different from all other species of *Dermacentor* as it is a one-host tick. Its hosts are the larger domestic and game animals, such as cattle, horses, elk, moose, and deer. The ticks are present on their hosts only during the winter season, from September (usually) to early spring. The females lay their eggs on the ground, and when they hatch the larvae bunch together and are torpid during the warmer months; they become active at the approach of cold weather and seek out their hosts. Once attached, the tick completes its life cycle, only dropping when the adult stage is reached. This tick is widely distributed throughout North America and is frequently a serious pest of elk, moose, deer, and horses in its northern range in Canada. Thomas and Cahn (1932) report this tick to be a vector of a serious disease of moose in northern Minnesota and adjacent regions of Ontario.

THE GENUS *IXODES:* The species of this genus can be recognized readily by the anal groove curving around the anus in front. They are inornate, without eyes, and lack festoons. Males differ from females: they have ventral plates, 1 median, 1 anal, and 2 adanals (a pregenital and 2 epimeral plates may also be present); they are normally much smaller than the females. Over one hundred species have been described, but probably not over fifty can be considered good species. Comparatively little is known about their biology, distribution, bionomics, or hosts; a few species have been thoroughly studied.

Ixodes ricinus (Linn.) [2] is probably world-wide in distribution. Its hosts include cattle, dogs, horses, cats, deer, foxes, sheep, man, and other animals. It is a three-host tick. As it is the vector of louping ill of sheep in Great Britain (northern England and Scotland) it has been studied intensely in recent years. The tick appears to require a moist climate (70 to 80 per cent relative humidity) for its best development. MacLeod (1932–1936) reports the female lays 2400 to 3200 eggs; the eggs hatch in 4 to 10 weeks; the larval and nymphal stages are usually completed in from 16 to 20 weeks. He found the males and females can live nearly two years, the larvae two years, and the nymphs over a year, without feeding. The rapidity of development depends on the various stages finding available hosts. It is probable that it normally requires almost a year for the complete life cycle. Recently this tick has been found to transmit louping ill of sheep in the U.S.S.R. (Silber and Shubladze, 1945). Louping ill has also been reported from man. This tick is also the most important vector of piroplasmosis (*Babesia bovis*) of cattle in Europe.

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[2] Cooley (1945) does not consider that this tick occurs in North America.

Ixodes pacificus Cooley and Kohls (usually called *californicus* Banks) closely resembles *Ixodes ricinus*. It occurs commonly along the Pacific coast from southern British Columbia to Mexico west of the Cascade Mountains. The adults attack a wide range of animals including man. The immature stages also attach to cold-blooded animals and birds. As it is a three-host tick, it may prove of some importance in the transmission of disease.

Ixodes cookei Pack. is a common tick in the eastern United States and occurs on a variety of animals such as woodchucks, foxes, squirrels, skunks, weasels, dogs, and cows. It is not an uncommon tick on humans. The author has nine records from humans: two ticks taken from the eyelids of children, two from the shoulders of adults, four from the head and neck, and one from below the breast—all were from the central New York region. This tick has not been studied to determine whether it can transmit any disease. *Ixodes holocyclus* Neum. occurs in India, Australia, and the East Indies. Its life cycle is quite similar to that of *I. ricinus*. It has a wide range of hosts, including man. *I. pilosus* is widespread in South and East Africa. The last two species are notorious for the production of "tick paralysis" in man and animals.

THE GENUS *AMBLYOMMA:* This is a large genus of ornate ticks; they abound principally in the tropical and subtropical regions. They may be recognized by the long palpi and hypostome; the second segment of the palpus is over twice as long as it is wide, and the hypostome is armed with teeth only on the apical half. Eyes and festoons are present. Although over ninety species have been described, Cooley (1944) lists only seven species from North America. The species are most abundant in South America and Africa and are very difficult to diagnose.

Amblyomma americanum (Linn.), the lone-star tick (Fig. 25), is easily identified by the solitary white spot on the posterior margin of the scutum of the female. It is widely distributed in the United States east of central Texas north to southern Iowa and east to the Atlantic seaboard. It is recorded as abundant in the Ozark region and occurs commonly along the south Atlantic coast and in the canebrakes of Louisiana and Mississippi as well as in wooded regions of many of the southern states. It is a three-host tick, and in its southern range it breeds throughout the year. The larvae and nymphs occur on a wide range of hosts including birds; all stages attack many different mammals such as cattle, horses, hogs, and man. Its bite is very painful and may be followed by suppurating sores. The larvae, nymphs, and adults can survive nearly a year or longer without food. This tick is a vector of Rocky Mountain spotted fever (Texas and Oklahoma), is a suspected vector of "Q" fever and tularemia, and is reported as a transmitter of a new clinical syndrome, "Bullis" fever.

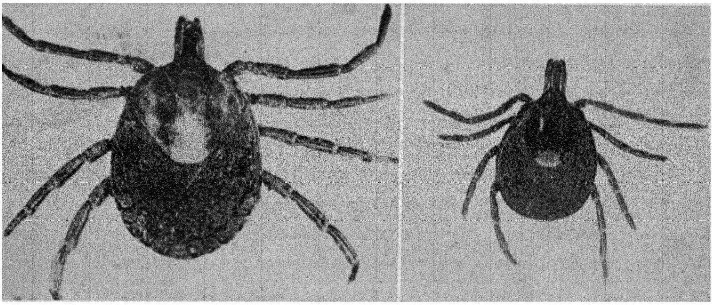

Fig. 25. Left: Amblyomma cajennense. Right: A. americanum. Adult females.

Amblyomma cajennense (Fabr.) is distributed from the southern tip of Texas south through Central America, Panama and south along the Atlantic seaboard to Argentina. Unlike the lone-star tick the scutum has an extensive pale pattern (Fig. 25), and the internal spur of coxa I is about one-half as long as the external spur. It is a three-host tick and all stages readily attach to man. Where it occurs in abundance, it is very annoying to all domestic animals and many wild animals, and man suffers very severely from its attacks. As the tick is very small (3 to 3.5 mm. in length in the female), it easily gains access through clothing. The bites are very deep owing to the long mouth parts and frequently develop into sores that are difficult to heal. In Brazil and Colombia it is the recognized vector of spotted fevers (Brazilian spotted fever and Tobia fever). These diseases are presumably identical with Rocky Mountain spotted fever, and *A. cajennense* may prove a suitable vector when this disease is introduced into southern Texas.

Amblyomma maculatum Koch is an important pest of livestock along the Atlantic and the Gulf coasts, extending from South Carolina west to Texas. It also occurs throughout South and Central America. The larval and nymphal stages attach to birds and some of the smaller wild mammals; the adults attach in the ears and when abundant produce inflammation and swelling. The points of attack furnish ideal places for infestation with screw worms, which may result in the death of the animals.

Amblyomma hebraeum Koch, the bont tick, is widespread in South Africa. It is a three-host tick and, in all stages, attaches to man as well as to many domestic and game animals. In its range it is a vector of tick-bite fever of man and heart water of cattle, sheep, and goats. Many other species of *Amblyomma* occur in Africa and are important pests of domestic and game animals, and some are vectors of serious diseases.

THE GENUS *RHIPICEPHALUS:* The ticks of this genus are practically always inornate, with eyes on the margins of the scutum and with festoons. When viewed dorsally the capitulum is generally hexagonal in outline. The males are smaller than the females and possess ventral shields. Over thirty species are recognized, and of these more than twenty are known from Africa. In North America there is one species, which is world-wide in distribution.

Rhipicephalus sanguineus (Latr.), the brown dog tick (Fig. 9), is widely distributed in the United States and occurs in most of the temperate and tropical regions of the world. It was first reported from southern Texas in 1912, and since then it has spread to most parts of the continent. It is primarily a pest of dogs and has not been reported as a pest of man in the United States. In the temperate climates this tick seeks warm places such as houses, dog kennels, and similar places where it may pass generation after generation. In warmer climates it occurs out of doors, often in great numbers. It is a three-host tick and all stages develop readily on dogs. Under favorable conditions the entire life cycle from the egg to the adult may be completed in less than two months. In the North this tick often becomes very abundant in private homes where dogs are allowed to wander at will. They may be found in cracks and on the walls, floors, and ceilings. They are difficult to eradicate. In some parts of the world, as about the Mediterranean region and in Africa, this tick is known to attach to man. It is also reported attacking man in Mexico. It is a vector of several diseases. It is known to transmit boutonneuse fever and Kenya tick typhus and has been shown experimentally to be capable of transmitting Rocky Mountain spotted fever and Spanish relapsing fever; it is also implicated in tick-bite fever and "Q" fever. Bustamente *et al.* (1946) have found this tick naturally infected with Rocky Mountain spotted fever in Mexico. It is an important vector of canine piroplasmosis (*Babesia canis*) or malignant jaundice of dogs; this disease is common in the Mediterranean region and South Africa and has recently been reported from Florida.

Other species of this genus are important vectors of serious diseases of domestic animals in various parts of Africa. *R. appendiculatus, R. capensis, R. evertsi,* and *R. simus* are vectors of East Coast fever of cattle; the last two are also involved in the transmission of red-water fever of cattle; *R. simus, R. sanguineus,* and *R. bursa* are vectors of bovine anaplasmosis (*Anaplasma marginale*); and other species are known to transmit several different diseases.

THE GENUS *HAEMAPHYSALIS:* The ticks of this genus are small, eyeless, and inornate but with festoons. The second segment of the palpus projects laterally at its base and gives the capitulum a triangular appearance in dorsal view. More than fifty species have been described, but only a few of them are known to play any part in disease transmission.

Haemaphysalis leporis-palustris (Pack.), the rabbit tick (Fig. 9), plays an intermediate but important part in the transmission of Rocky Mountain spotted fever and tularemia. According to Green and his associates (1943), the favorite host of this tick in all stages is the snowshoe hare, the second most important host is the ruffed grouse, and the cottontail rabbit is the third. In addition, this tick is reported from more than sixty species of ground-loving birds, from many different rodents, and occasionally from domestic animals. The larvae and nymphs are the stages most commonly found on birds. It is not known to attach to man; only one case has been reported by Brown (1946) in Alberta, Canada. The tick is a three-host tick and feeds, in the North, during the spring, summer, and autumn. It hibernates in all stages on the ground. In the South the tick is found on its hosts throughout the year. The life cycle may be completed in as short a time as 75 days, or it may be greatly prolonged if hosts and conditions are not favorable. All stages of the tick are capable of surviving long periods of starvation. The importance of this tick lies in its ability to transmit Rocky Mountain spotted fever and tularemia among the reservoir hosts. If infected the tick can transmit these diseases to susceptible hosts at each feeding. The rabbit tick is widely distributed from Alaska and Canada throughout the United States and Central and South America to Argentina.

Haemaphysalis leachi (Aud.) is an important tick with a wide distribution in Africa, Asia, and throughout the Australasian region. It is the vector of canine piroplasmosis (*Babesia canis*) and is reported as a transmitter of tick-bite fever in South Africa. *H. humerosa* of Australia has been shown to transmit "Q" fever among bandicoot rats, a natural reservoir of the disease, while *H. bispinosa* is thought to be one of the vectors to man. Other ticks are recorded as playing a role in the transmission and maintenance of this disease in Australia.

TICKS AND DISEASE

Our knowledge of ticks and the role they play in the causation of diseased conditions in man and other animals and in the transmission of pathogenic organisms has greatly increased during the past few years. Smith and Kilbourne (1893) were the first to prove that the ordinary cattle tick, *Boophilus annulatus* (Say), is the vector of Texas fever, red-water fever, or hemoglobinuria of cattle. Furthermore they showed that the organism *Piroplasma bigemina* is passed through the egg to the larva. Infection occurs when larvae descended from infected mothers feed on nonimmune cattle. This was the first demonstration of the passage of a pathogenic protozoan from the parent to the offspring. During the intervening years a large number of ticks have been shown to be the vectors of many serious diseases of man and other animals. At present the interrelations of ticks and disease may be roughly classified as follows:

1. Direct effects produced by their bites.
2. Causation of paralysis, known as "tick paralysis."
3. Hosts and vectors of pathogenic organisms.

TICK BITES

Tick bites are at times rather serious. In many domestic and game animals the loss of blood is often great; frequently the mass attack, especially in young animals, results in death or weakness, which exposes them to disease or destruction by their enemies. Moose and elk have frequently been reported as weak and dying from mass attacks of *Dermacentor albipictus,* and young cattle are undoubtedly killed by attacks of *Boophilus annulatus.* When ticks bite there is injected into the wound the secretions of the salivary glands, which in some cases are known to possess an anticoagulin and in others a toxin. Whatever may be present, the bites of certain species produce ugly ulcerations, which are difficult to heal and which offer ideal conditions for the invasion of pathogenic organisms or the attacks of myiasis-producing flies. Widely varying effects are reported by different workers. This should be expected since insect bites affect different people in the most varied ways. When a tick has buried its capitulum deeply, it should be removed with great care. Holding the lightened end of a cigarette to the tick will usually cause it to loosen its hold. It should then be carefully removed and not crushed by hand but stamped on or placed in alcohol. Crushing it might result in infection if the tick happened to be carrying some pathogenic organisms. Another method of tick removal (said to be effective by those using it) is to place a piece of adhesive tape over the tick, attaching it firmly on both sides of the tick. This will cause the tick to withdraw its mouth parts and it then can be removed without tearing the flesh. The wound should be treated by some antiseptic such as alcohol, and, if a physician is available, he should be consulted. Should infection result the physician will have a better chance to give the correct treatment. Table 3 lists ticks that are recorded as producing severe wounds on man by their bites. The bites of many other ticks are annoying, but little information can be found about them.

Table 3. Ticks whose bites may have severe effects on man.

Species	Effect of bite	Authority
Argas mianensis	Severe; produces fever	Nuttall and others
A. brumpti	Bite severe and wound pruriginous for long time. After 25 years nodules still persist at location of bite	Brumpt (1927)
Ornithodoros savignyi	Extensive ecchymosis	Patton (1913)
O. gurneyi (Australia) on Kangaroo	Reported to cause paralysis, blindness, and unconsciousness	*Man. Trop. Med.* (1945)
O. turicata	Effects severe	Nuttall (1908) and others
O. rostratus	Bites severe	Davis (1945)
O. talaje	Effects severe	Nuttall and others
O. moubata	Bites of nymphs, severe?	Nuttall (1908)
O. lahorensis	Bites severe	Vogel (1927)
O. brasilienses	Bites severe	Davis in *Man. Trop. Med.*
Ixodes ricinus	Bites often accompanied by paralysis	Nuttall (1908)
I. ricinus (?)	Severe, followed often by ulceration or glandular involvement	Mail and Gregson (1938)
I. pacificus (*californicus*)	Bite severe and reactions often follow	Various authors
Amblyomma cajennense	Severe, often followed by sores difficult to heal	Various authors

TICK PARALYSIS

Tick paralysis is a peculiar disease found mostly in young children and domestic animals, such as sheep, dogs, cattle, and goats, when attacked by certain species of ticks. The paralysis is usually preceded by muscular weakness and inability to co-ordinate the movements of the legs, followed in a few hours by a more or less complete flaccid paralysis of the lower limbs. The paralysis extends rapidly upward, involving the arms and neck; speech and deglutition become difficult; and, if the tick is not found and removed, death results from respiratory paralysis. In many cases a marked rise in temperature occurs. In North America the ticks involved are *Dermacentor andersoni* and *D. variabilis;* there is also a possibility that a species of *Ixodes* may play a part in British Columbia. When these ticks attach at the base of the skull, on the head, or along the spine, paralysis may result. If the tick or ticks are removed before paralysis reaches the respiratory state, recovery is usually prompt and rapid. Todd (1914) reviews the history of tick paralysis in British Columbia. For a long time practicing physicians in British Columbia have known this disease was associated with tick bites. Todd (1914) gives the records of ten cases reported by different physicians, and all except one recovered promptly after the removal of a tick (*Dermacentor andersoni*). He also gives details of a series of experiments with this tick; he obtained paralysis in a puppy and lambs but failed with monkeys and guinea pigs. Hadwen (1913) and Nuttall (1914) confirmed these results by producing paralysis in sheep and dogs by the bites of *D. andersoni.* McCormack (1921) records 13 cases of tick paralysis in young children and one of a girl 21 years old. All recovered when the ticks were discovered and removed except in one case in which the tick was not noted till after death. Nuttall (1914) lists 13 cases as observed by Dr. Temple in Oregon. Cogswell (1923) lists 6 cases in children in Montana. Mail and Gregson (1938) report 26 cases from British Columbia during the period from 1910 to 1931; of these four died. *Dermacentor andersoni* was the tick involved. They also state that they have records of at least 150 cases from the province. Robinson and Carroll (1938) report a single case of tick paralysis in a young girl from Georgia caused by the bite of *Dermacentor variabilis.* Recovery was rapid when they found and removed two ticks from the parietal region of the skull. Gibbes (1938) lists a case of a young woman in South Carolina who was suffering from a peculiar paralysis when she was admitted to a hospital. The accidental finding and removal of a tick from the back of the scalp brought almost immediate recovery. The tick was undoubtedly *Dermacentor variabilis.* Undoubtedly physicians have treated many other cases of which we have no record. Ticks do not, in all cases, produce paralysis when they attach to young children, but, when children show unusual weakness accompanied by inability to co-ordinate the movements of the legs, search should be made at once for ticks and they should be carefully removed.

Tick paralysis also occurs among sheep. Hadwen (1913) reports many cases among lambs in British Columbia. Hearle (1933) reports an outbreak of paralysis among steers in British Columbia. Out of 900 steers 100 became paralyzed and 65 died. Moillett (1937) records 200 steers stricken in a herd of 638 in the same province; of these 26 died. In all cases *D. andersoni* was the tick involved. In Australia paralysis in lambs, dogs, and children is caused by *Ixodes holocyclus* Neum. Ferguson (1924) reports eight deaths of children in Australia from tick paralysis, all caused, he believes, from the bites of *Ixodes holocyclus.* Ross (1926) records numerous experiments with this tick on dogs but was unable to determine the exact agent producing paralysis and death. Tick paralysis has also been reported from South Africa caused by the bites of *Ixodes pilosus* Koch. Veneroni (1928) reports two cases of tick paralysis in Italian Somaliland from bites on the neck by the tick *Rhipicephalus simus* Koch. In Europe *Ixodes ricinus* (Linn.) is known to cause a paralysis by its bites.

This peculiar ascending motor paralysis has been reported from widely separated regions of the world and is caused by at least six different species of ticks. As the onset of the disease may easily be mistaken for poliomyelitis, it is essential that in all cases of paralysis of children search should be made for the presence of ticks. As a prophylactic measure all people, especially children, that camp, play, or live in tick-infested regions should be carefully examined each day for ticks. The head should be combed with care since the small unengorged ticks are not easily located. If ticks are found, report to a physician so that any sign of sickness may be treated at once. In all cases remove the ticks so that the head is not left buried in the wound. If the head is left, have a physician remove it.

TICKS AS VECTORS AND HOSTS OF PATHOGENIC ORGANISMS AND VIRUSES

Human Diseases

During the past fifty years ticks have been discovered to be the active vectors and hosts of many animal and human diseases. Smith and Kilbourne (1893) first demonstrated the relation of *Boophilus annulatus* (Say) and hemoglobinuria or red-water fever of cattle. The causative agent of this disease is a minute protozoan, *Piroplasma bigemina,* which lives within and destroys the red corpuscles. It is a very serious disease, and no adequate treatment is known except the control of the ticks. A similar disease of cattle in Europe, caused by *Babesia bovis,* is transmitted by the ticks *Ixodes ricinus,* *I. hexagonus,* and probably other species. Numerous other diseases of animals are transmitted by ticks, but space does not permit of more than a mention here.

RELAPSING FEVERS OF MAN (Tick-borne): In recent years a large number of relapsing fevers, caused by *Spirochaeta* spp. (often referred to under the generic names *Spirillum, Treponema,* or *Borrelia*) have been recognized by different workers. These relapsing fevers are characterized by repeated attacks of fever, the attacks lasting from three to five days. The periods of apyrexia vary from five to ten days. The causative agents of these fevers are species of *Spirochaeta* that are present in the blood, cerebrospinal fluid, and other body fluids and are most abundant during attacks of fever. During the apyrexial periods they may apparently be absent from the blood stream though experimental infection work has demonstrated their presence. The vectors of the various species of *Spirochaeta* are ticks and lice, though other arthropods may at times play a part. The presence of the spirochetes in the blood stream during the entire infection period is of great significance, especially when prophylactic measures are considered. *Spirochaeta recurrentis* (Lebert), often referred to as *S. obermeieri,* was the first species observed to infest the blood of man. It was first seen by Obermeier in 1868 and was described and named by Lebert in 1874. Ross and Milne (1904) were the first to demonstrate that a peculiar fever of West Africa was caused by a spirochete (now known as *Spirochaeta duttoni*) and that the spirochete was transmitted to man by a tick, *Ornithodoros moubata* (Murray). Later, but independently, Dutton and Todd (1905) demonstrated that *O. moubata* was the vector of this spirochete. Furthermore they proved that the newly hatched offspring of infected ticks were capable of transmitting the disease. Since then it has been shown that infection in the tick can pass through the eggs even to the third generation. At present numerous species of spirochetes have been described from the blood of man and animals. More than 12 species have been described as occurring in man, but there is no general agreement that these are all distinct species. Some authorities consider them to be nothing more than strains of the one species, *S. recurrentis.*

Tick relapsing fevers are widely distributed throughout the world, being recorded from Europe, Asia, Africa, North, South, and Central America, and Mexico. In North America tick relapsing fever is known from at least 13 western states and the southern part of British Columbia. Though relapsing fever was first recognized by Meader (1915) in Colorado and other physicians in California (1922) and Texas (1927), it was not till 1930 that Weller and Graham showed it to be tick-borne. They demonstrated that *Ornithodoros* *turicata* was the vector. Since then at least two other species of *Ornithodoros* have been recognized as active vectors in the United States. In practically all cases the spirochetes are passed from generation to generation through the eggs, and Davis is of the opinion that the active reservoirs of the spirochetes are the ticks rather than the susceptible animals such as rodents on which so many of the ticks feed. Table 4 will give in brief form the known tick vectors and the present distribution of the disease. The distribution of the ticks is usually much more extensive than that of the disease. Undoubtedly other species are involved, but data on them are not available.

Table 4. Tick relapsing fever.

Vector	Distribution of ticks	Known occurrence of disease (and name of spirochete strain)
Ornithodoros turicata	Southwestern U.S.A., Florida, and Mexico	New Mex., Kansas, Okla., Texas, Mexico (*S. turicatae*)
O. hermsi	Calif., Col., Ore., Wash., Nev., Idaho (At high elevations, 3000 ft.+)	Calif., Col., Idaho, Nev., Wash., British Columbia (?) (*S. hermsi*)
O. parkeri	Nine western states from Wash. to southern Calif. and east to Mont. and Col.	California. (Ticks with spirochetes also taken in Idaho, Mont., Nev., Wyo., and Utah) (*S. parkeri*)
O. talaje	Calif. to Kansas, south to Argentina	Panama, Colombia, and Guatemala (*S. venezuelensis*)
O. rudis (*venezuelensis*)	Panama, Colombia, Venezuela, Paraguay (A house tick)	Panama, Colombia, Venezuela (*S. venezuelensis*)
O. moubata	Africa from Lake Chad east to Red Sea and south to Cape Province	Throughout the range of the tick (*S. duttoni*)
O. savignyi	Same area as *O. moubata,* also North Africa, Arabia, and India	Probably throughout its range (*S. duttoni?*)
O. erraticus	Western littoral of Mediterranean, Spain south to Senegal in Africa	Southern Spain and parts of Africa (*S. hispanicum*)
O. tholozani (*papillipes*)	Caucasus, Iran, Syria, Palestine, Cyprus	Cyprus, parts of Russia (*S.* sp.?)
O. nereensis	Turkmenia (Russia)	Turkmenia (Russia) (*S.* sp.?)

The method of transmission of the spirochetes by the various species of ticks is not known in all cases. The ticks obtain the spirochetes when feeding on the blood of animals that are infected. In the tick the spirochetes multiply by transverse fission. The spirochetes invade the tissues and body cavity of the tick. When an infected tick bites a new host, the spirochetes gain entrance either through the coxal fluid glands, which eject their secretion (as in *O. moubata*) or by way of the bite as in *O. turicata, O. parkeri, O. hermsi, O. tholozani,* and probably others (Davis, 1945).

ROCKY MOUNTAIN SPOTTED FEVER: Ever since the settlement of Montana there has appeared in certain regions, particularly the Bitter Root Valley, a peculiar and very fatal disease of man. The disease was first recognized here about 1890. It is characterized by sudden onset, a high fever, severe arthritic and muscular pains, and a profuse petechial eruption in the skin, appearing first on the ankles, wrists, and forehead but later usually spreading all over the body. In fatal cases the disease runs a rapid course, the patient dying from the sixth to the twelfth day. If the fever falls and the patient lives two weeks, recovery is usually rapid. There are two strains of the disease, a mild and a virulent type, and these appear to be present in most of the regions in which it occurs. The mortality rate varies from about 80 per cent for the virulent strain to about 4 to 6 per cent for the mild strain. This disease is designated "Rocky Mountain spotted fever" from its place of apparent origin. It is noncontagious, highly infectious, and transmitted to man by ticks. Wilson and Chowning (1902–1904) first advanced the theory that the disease was tick-borne and Ricketts (1906–1909) and his co-workers demonstrated that the disease is primarily an infection of small mammals (rodents); that large mammals, except man, are not susceptible; and that the tick, *Dermacentor andersoni,* is the transmitting agent for man. Wolbach (1919) described and named the parasite *Dermacentroxenus rickettsi.* For many years this disease was known only from a restricted area in the Rocky Mountain region. Rumreich, Dyer, and Badger (1931) demonstrated the disease in the eastern United States and reported cases from rural areas in Delaware, Maryland, Pennsylvania, Virginia, North Carolina, and the District of Columbia during the summer of 1930. Later they proved that the vector was the dog tick, *Dermacentor variabilis.* Since then the disease has been found rather widespread throughout the United States. At present the disease is also known from western Canada (British Columbia and Alberta) and many parts of South America and Mexico. In South America this disease has been called exanthematic typhus of São Paulo, Tobia fever of Colombia, Choix or Pinta fever in Mexico, and Minas Geraes typhus in Brazil. The tick vector in South America is *Amblyomma cajennense.*

The relation of ticks to this disease may be considered under two headings: maintenance in nature and transmission to man.

MAINTENANCE IN NATURE: The following species of ticks are known to transmit, or can transmit experimentally, the rickettsiae among the reservoir hosts (mainly rodents): *Dermacentor andersoni* (mainly by the larvae and nymphs); *Dermacentor variabilis* (all stages); *Dermacentor occidentalis* (all stages); *Rhipicephalus sanguineus*[3] (experimentally); *Amblyomma americanum* (all stages); *Amblyomma cajennense* (experimentally and probably in nature); *Ornithodoros parkeri* (all stages experimentally); *Ornithodoros nicollei* (all stages, experimentally). In addition, all these ticks pass the rickettsiae through the eggs to their young so that the natural reservoir in rodents can be maintained or greatly increased. Another tick that is undoubtedly very important in many areas is the rabbit tick, *Haemaphysalis leporis-palustris.* This tick does not attack man, but it can transmit the rickettsiae from rabbit to rabbit and thus maintain an adequate source for those ticks that bite man and also feed on rabbits.

TRANSMISSION TO MAN: Only those ticks that become infected and feed on man can transmit the disease. *Dermacentor andersoni* (adults) is the vector throughout its range (western Canada and western United States); *Dermacentor occidentalis* is probably a vector in the United States in western California and parts of Oregon; *Amblyomma americanum* (all stages) is a vector in some parts of the United States (known only at present as a vector in Texas and Oklahoma); in Brazil and Columbia *Amblyomma cajennense* is reported as the vector. In addition, other species may play a part as *Ornithodoros parkeri,* which Davis (1943) has shown to be an effective transmitter in all stages and through the egg even to the fourth generation. The same worker (1943) has shown that *Ornithodoros nicollei* is a good experimental vector of the rickettsiae of the spotted fevers of Brazil, Colombia, and Mexico in all stages and through the egg to the next generation. As this tick feeds readily on man and dogs, it is probably a vector in its range.

The incubation period in man after infection by a tick varies from 2 to 12 days. In recent years a vaccine has been developed that gives good promise. It is said to be effective for nearly one year, and if it does not confer entire immunity it at least reduces to a minimum the danger of a fatal termination of the disease.

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[3] Recently found naturally infected in Sonora, Mexico (Mariotte *et al.,* 1945).

TULAREMIA: Tularemia is a plaguelike disease of rodents, particularly of rabbits and hares, caused by *Pasteurella tularensis* (*Bacterium tularense*). The disease was discovered in rats in California by McCoy in 1910. The bacterium was isolated from squirrels and described by McCoy and Chapin in 1912. Francis (1919, 1920) demonstrated that the so-called "deer-fly fever" of man in Utah and the plaguelike disease of rodents are identical and caused by the same organism; he later (1921) named the disease "tularemia." The disease is highly infectious to man and is transmitted by various arthropods either by their bites, their crushed bodies, or their feces or by the tissues or body fluids of infected rodents; it is also occasionally water-borne. The disease is widespread in the United States and is reported from the following countries: Japan (1925), Russia (1928), Norway (1929), Canada (1930), Sweden (1931), Austria (1935), Germany, Czechoslovakia, and Turkey (1936), Alaska (1937, no human cases but the organism was isolated from rabbit ticks), and from Tunisia.

NATURAL RESERVOIRS: There are numerous natural reservoir hosts. Burroughs *et al.* (1945) list 44 hosts from the world, distributed among birds, insectivores, rodents, carnivores, and ungulates. They list 4 birds (ruffed grouse, bobwhite, sage hen, and horned owl), 3 carnivores (cat, dog, and coyote), 20 rodents, and sheep from the United States. Jellison and Parker (1945) present rather conclusive evidence that the main source of human infection in the United States is from cottontail rabbits (*Sylvilagus* spp.) particularly *S. floridanus.* Of the 14,000 cases reported in the United States (up to 1942) fully 90 per cent are traceable directly to infection from cottontail rabbits; only 40 cases occurred beyond the range of these rabbits. Jack rabbits are known reservoirs and are an indirect source of human infection through the agency of ticks and deer flies. In the same manner many rodents are indirect sources of human infection.

TRANSMISSION TO MAN: Human infection is mainly through contact with reservoir hosts, particularly rabbits. The bacterium (*Pasteurella tularensis*) is so infectious that it can pass directly through the human skin, and thus man is readily infected by handling infected animals, their flesh, or body fluids; by contact with the fecal wastes or body fluids of the vectors; by eating partially cooked infected rabbits, squirrels, and others; or by handling or drinking infected water. Jellison and Parker state that 90 per cent of the human cases in the United States result from handling infected rabbits; the other 10 per cent of the cases are traceable to handling other infected rodents, sheep, game birds, or other animals or by transmission by arthropods. Certain arthropods play an important part in maintaining this natural reservoir and also in transmitting the disease to man. Francis (1921) was the first to demonstrate the transmission of tularemia from infected animals (the jack rabbit) to man by the deer fly, *Chrysops discalis* (Fig. 161). Parker, Spencer, and Francis (1924) demonstrated that *Dermacentor andersoni* and *Haemaphysalis leporis-palustris* could transmit the disease and that the bacterium passes from stage to stage of the ticks. In 1926 Parker and Spencer reported the survival of the bacterium through the egg to the young of *Haemaphysalis leporis-palustris* and *Dermacentor andersoni.* Philip and Jellison (1934) showed stage-to-stage and generation-to-generation survival of this bacterium in *Dermacentor variabilis. Dermacentor occidentalis* and *D. marginatus* have also been shown to play some part in this disease complex.

Although most of the human infection in North America is traceable to contact with rabbits, it must be borne in mind that ticks, particularly *Haemaphysalis leporis-palustris, Dermacentor andersoni, D. variabilis,* and other bloodsucking arthropods, are of great importance in maintaining the disease among the natural reservoirs. Furthermore the disease can be water-borne as shown by Scott (1940) and Jellison *et al.* (1942) in the case of beavers and by Karpoff and Antonoff (1936) in the case of water rats in Russia. In both instances the water was shown to be highly infectious when handled or drunk. Mosquitoes may also play a part in the infection of man and among the reservoir hosts, as shown by Philip (1932).

AUSTRALIAN "Q" FEVER, AMERICAN "NINE-MILE FEVER": "Q" fever was first recognized as a distinct entity by Derrick (1937) in Australia. It occurred among meat handlers and slaughterers in a restricted area about Brisbane. The causative organism was isolated and described as *Rickettsia burneti* by Burnet and Freeman (1937). "Nine-Mile fever" was recognized near Nine Mile Creek in Montana in 1938, and the infectious agent was isolated from the tick *Dermacentor andersoni* by Davis and Cox (1938); the human case (a laboratory worker) was described by Dyer (1938). Cox (1939) named the organism *Rickettsia diaporica.* It now seems well established that these two isolated diseases are identical.[4] In Australia the reservoir appears to be in bandicoot rats (*Isodon torosus*), three out of 103 tested being naturally infected. All species of bush animals tested proved susceptible to infection. The tick *Haemaphysalis humerosa* taken from bandicoots proved infectious, and bandicoots in certain areas showed a high agglutination rate (34 per cent). Although this tick does not normally bite man, it is suggested that it maintains the reservoir and that *Ixodes holocyclus* (which readily bites bandicoots, man, and other animals) may transmit the disease among the bandicoots and to man. The rickettsiae develop in the epithelium lining of the gut of the tick so that the lumen and fecal wastes are heavily charged. The feces are highly infective, even when dry and powdery, to broken or injured skin. Transmission is only through fecal wastes of infected ticks entering the wound made by the bite or by the dry infective fecal wastes gaining access to wounds or by way of the respiratory tract. Other potential tick vectors are *Haemaphysalis bispinosa* and *Rhipicephalus sanguineus.*

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[4] Recently the generic name has been changed to *Coxiella.*

In North America *Rickettsia diaporica* has been isolated from *Dermacentor andersoni* in Montana and Wyoming, from *Dermacentor occidentalis* in Oregon and California, and from *Amblyomma americanum* in Texas (Liberty County). Davis (1943) demonstrated that *Ornithodoros moubata* could be infected by feeding on infected guinea pigs and could transmit the infection by feeding up to 428 days following the infective feeding, and that transmission through the eggs was obtained to the F_2 generation. The infective agent was conserved in the tissues of the tick for at least 670 days. With *O. hermsi* transmission took place by feeding up to 772 days after the infective meal, and the infectious agent was conserved in the tissues for at least 979 days; there was no transmission through the egg.

In Australia 176 cases in humans with three deaths are recorded up to 1942. In North America, cases (15, with one death in Washington, D.C.) have occurred in laboratory workers, and the infection is believed to be due to the inhalation of infected tick feces or dust from cultures while the persons were working with experimental animals. In cases involving the respiratory tract the disease is more serious. Recently an outbreak was reported at Amarillo, Texas, among slaughter-house workers (55 cases). Elkland (1947) records a case in Montana probably contracted from *Dermacentor andersoni* in the wild. Huebner *et al.* (1948) located an endemic center of "Q" fever in southern California (117 cases during 1947). They also report recovering *Rickettsia burneti* from raw milk in several dairies. Jellison and his co-workers (1948) recovered the organism *Rickettsia (Coxiella) burneti* not only from raw milk but from butter made from unpasteurized milk. They also found the spinose ear tick, *Otobius megnini* (Dugès), naturally infected.

During World War II extensive outbreaks of "Q" fever occurred among Allied troops in Italy and Axis troops in the Balkans (Balkan grippe) and in Greece. Cases were also reported from Panama. Workers in research laboratories, especially among those handling the cultures of *Rickettsia burneti,* were infected. As a result of intensive studies of these outbreaks it seems established that there may be several strains of "Q" fever, but all appear to be identical from the standpoint of reciprocal cross immunity, complement fixation, and agglutination absorption tests. Unfortunately nothing was learned regarding the sources of the infection, the animal reservoirs, or the methods of transmission unless we accept the one known method—the inhalation of the infectious agent (*Amer. Jl. Hyg.*, 44, 1946).

COLORADO TICK FEVER: This disease is of unknown etiology. It is reported from various portions of the mountainous areas of Colorado, wide areas of Wyoming, and parts of Idaho. Parker *et al.* (1937) state that it was first observed in 1907 but not regarded as a distinct entity till 1930. The disease is associated with the bite of *Dermacentor andersoni* but is distinct from Rocky Mountain spotted fever; there is no rash and the fever is of the remittent type. The disease rarely proves fatal.

BULLIS FEVER: This peculiar disease is named after Camp Bullis in Texas, where the first cases were recognized by Woodland *et al.* (1943). In 1943 over 485 cases were isolated among the troops; later Anigstein and Bader reported that some 1000 cases were observed. All reports indicate that the vector is the tick *Amblyomma americanum,* as practically all cases had numerous tick bites and this tick is the common and most abundant tick in the area and readily bites man. Steinhaus and Parker (1944) report a filter-passing agent from the tick *Haemaphysalis leporis-palustris,* taken from rabbits, but the authors do not conclude that this virus may be the causative agent of Bullis fever.

TICK TYPHUS: Tick typhus has been described from widely separated regions. The etiology of the disease is unknown. The disease is reported from Russia (central Siberia), where Bocharova (1945) reports that it is tick-borne and the vector *Dermacentor nuttalli* Olenev; he also found natural infection in this species in the wild. Natural infection was found in a number of rodents, including the domestic rat. Singh (1943) reports a case of typhus fever from Meerut, India, that Megaw (1943) calls a typical case of tick typhus. Walsh (1945) reports an epidemic of tick typhus in East Africa, and Tovar (1945) indicates that the disease is widespread in the Americas but not yet detected. It would seem that this disease entity is not well understood. Kenya tick typhus is said to be almost similar to boutonneuse fever.

BOUTONNEUSE FEVER (Fièvre Exanthématique de Marseille): This disease was first reported from Tunisia by Conor and Bruch (1910). It is now known to occur all along the Mediterranean littoral from Portugal to Romania, and it has recently been reported from Ethiopia. The causative organism has been described by Brumpt (1932) under the name *Rickettsia conori.* This organism has been recovered from the tick *Rhipicephalus sanguineus,* which is the known vector throughout the Mediterranean region. The reservoir hosts are the dog (most important), certain rodents as the spermophile *Citellus citellus,* the white rat, and mice. In the tick the rickettsia is transmitted from stage to stage and also through the egg to the larvae. The disease belongs to the "spotted-fever group."

Kenya tick typhus is thought to be identical with boutonneuse fever, and Roberts (1935) has shown that *Rhipicephalus sanguineus* is the vector in Kenya of what is frequently called "tropical typhus." The etiological agent has been described as *Rickettsia rickettsi conori.*

SOUTH AFRICAN TICK-BITE FEVER: This disease is closely related to the spotted fevers and is caused by a rickettsia, variously known as *Rickettsia rickettsi conori* or as a distinct variety, *R. r. pijperi.* It was recognized as a distinct clinical disease in South Africa sometime before 1930. Gear (1938, 1939) reports the disease in the Witwatersrand as severe, the reservoir being dogs and the vector the dog tick, *Haemaphysalis leachi. Amblyomma hebraeum* is also a vector, but it is stated that only the larval stage transmits the disease. The disease is nearly always associated with tick bites, the primary sore being described as a *tache noire,* and is accompanied by lymphadenitis. The dog tick, *Haemaphysalis leachi,* can transmit the disease in all stages and also by transovarial transmission through the egg; it is thus considered a reservoir of the disease. *Rhipicephalus sanguineus* is also reported as a potential vector. The distribution of the disease is not fully known.

RUSSIAN SPRING-SUMMER ENCEPHALITIS OR TICK-BORNE ENCEPHALITIS: This is the only human encephalitis known to be transmitted by ticks. It is recorded from parts of European Russia, Siberia, and parts of the maritime province of the Far East of Russia (always in well-demarcated virgin-forest regions). Various Russian investigators have shown that the tick *Ixodes persulcatus* Schulze is the natural vector. This tick occurs only in the forested regions, and the disease is transmitted to those who work in the forests. The tick has a two- or three-year cycle, and infection of the ticks occurs when they feed on the wild rodents that are the reservoirs. The virus is transmitted in the ticks from stage to stage and to the young through the eggs. Russian workers have shown that there are two peaks of infection, one in the spring and another in the summer. The first is from the feeding of the overwintering ticks, and the second is probably from the young that hatch from eggs laid during the spring months. There are indications that *Dermacentor silvarum, Haemaphysalis concinna,* and *H. japonica* may also serve as vectors since they have been found naturally infected.

ST. LOUIS ENCEPHALITIS: See pages 95, 367.

Animal Diseases

In addition to the human diseases many diseases of domestic and game animals are also transmitted by ticks. A few of these may be mentioned here.

PIROPLASMOSIS, RED-WATER FEVER, TEXAS FEVER, OR HEMOGLOBINURIA OF CATTLE: For a brief statement see page 58. In North America this disease (caused by *Piroplasma bigemina*) is transmitted by *Boophilus annulatus;* in Australia, the Philippine Islands, the Dutch East Indies, India, and parts of South America by *Boophilus australis;* and in South Africa by *Boophilus decoloratus. Boophilus microplus* is the vector in parts of South America, the West Indies, and probably other parts of the world. In East Africa this disease is also transmitted by *Rhipicephalus appendiculatus* and *R. evertsi.* In Europe a similar disease caused by *Babesia bovis* is transmitted by *Ixodes ricinus.* The etiological agent is transmitted from larva to nymph, from nymph to adult, and through the egg to the young. Malignant jaundice of dogs is a serious disease caused by *Babesia canis* and is transmitted by the brown dog tick (*Rhipicephalus sanguineus*) in the United States (Florida, where it was first discovered in North America in 1934), Asia, North Africa, and India; by *Dermacentor reticulatus* in Europe; and by *Haemaphysalis leachi* in South Africa. The parasite is passed by infected females through the egg to the larvae. "Carceag" of sheep and goats is caused by *Babesia motasi.* The disease occurs in eastern and southeastern Europe and its known vector is *Rhipicephalus bursa,* a one-host tick. The etiological agent is passed through the egg to the larvae, but infection is said not to take place till the tick has reached the adult stage on its host. Two diseases of horses are caused by species of *Babesia. Babesia caballi* is reported from southern and southeastern Europe and from the Caucasus region of Russia. The disease is very similar to Texas fever and *Dermacentor reticulatus* is the vector. *Babesia equi* occurs in southern Europe, Africa, southern Asia, and South America. In South Africa *Rhipicephalus evertsi* is the known vector. In adult horses and other members of the Equidae the disease (biliary fever) is highly virulent. Species of *Babesia* have been described from many other animals, but little is known about them or their vectors.

ANAPLASMOSIS: Theiler (1910) recognized the small, coccuslike bodies on the periphery of many of the red blood cells of cattle suffering from a specific disease (now known as "anaplasmosis") and named them *Anaplasma marginale.* These had previously been seen by Smith and Kilborne (1893), who did not correctly interpret them. In reality they had animals suffering from the two diseases, anaplasmosis and piroplasmosis. These two diseases are now well recognized, and anaplasmosis has been found in at least 22 states of our country as well as in South Africa. The disease is restricted to cattle and frequently proves very serious, with a mortality varying from 5 per cent to over 50 per cent. Ticks are the important vectors, and numerous species have been incriminated. Rees (1934) lists the following: *Boophilus annulatus, B. microplus, B. decoloratus, Dermacentor andersoni, D. variabilis, Hyalomma lusitanicum, Ixodes ricinus, I. scapularis, Rhipicephalus sanguineus, R. bursa,* and *R. simus.* To these can be added *Dermacentor occidentalis, D. albipictus,* and some others of doubtful proof. At the present time only *Boophilus annulatus, Dermacentor andersoni,* and *D. occidentalis* have been proved capable of transmitting the etiological agent to their offspring through the egg. In addition, many bloodsucking flies may act as mechanical carriers, such as the Tabanidae (at least seven species), and mosquitoes (several species). Probably one of the most important methods of transmission is from infected surgical instruments used in dehorning, bloodletting, castrations, etc.

EAST COAST FEVER: A serious disease of cattle largely confined to the eastern coastal region of Africa though it is reported from India and Transcaucasia is East Coast fever. It is caused by a minute protozoan, *Theileria parva.* This parasite occurs in the red blood cells, but the schizogonous cycle takes place in the spleen, lymph nodes, and some other organs. When the stage in the red blood cells is taken by ticks, particularly *Rhipicephalus appendiculatus,* it undergoes a complicated life cycle in the tick and finally infected forms are found in the salivary glands (Cowdry, 1932). Transmission takes place when an infected tick feeds on a susceptible animal. There is no transovarial passage of the parasite. Infection can pass from larvae to nymphs and nymphs to adults. Other proven vectors are *Rhipicephalus evertsi, R. simus* (only in adults), and a *Hyalomma* species closely allied to *impressum.*

FOWL SPIROCHETOSIS: This is a serious disease of fowls caused by *Spirochaeta gallinarum* Blanchard (*marchouxi* Nuttall). Its primary vector is the soft tick, *Argas persicus.* The disease is recorded from Brazil, Egypt, the Sudan, India, Australia, Europe (Germany), and the Transcaucasus region. The fowl mite, *Dermanyssus gallinae,* has been suspected as a vector, but the work of Rastegaieff (1936) would seem to disprove this idea, though Hungerford and Hart (1937) indicate that this mite may serve as a mechanical transmitter. Zulzer (1937) states that mosquitoes (which species?) serve as vectors and that there is a cyclical development in them.

OTHER DISEASES: There are other diseases of domestic animals which are transmitted by ticks, such as Nairobi sheep disease transmitted by *Rhipicephalus appendiculatus* and *Amblyomma hebraeum,* louping ill of sheep transmitted by *Ixodes ricinus,* heartwater of sheep, cattle, and goats in Africa transmitted by *Amblyomma hebraeum* and *A. variegatum,* and some others about which little is known.

TICK CONTROL

At the present time no adequate specific treatments are known for tick-borne diseases of man and animals except for the relapsing fevers of man. The intravenous injection of neoarsphenamine or other arsenic compounds usually brings about the complete elimination of the spirochetes of relapsing fevers. However, the disease runs a tedious course, and prophylactic measures are to be preferred rather than treatment after infection. In the case of malignant jaundice of dogs (caused by *Babesia canis*) and in illnesses caused by some of the other larger species of *Babesia,* the administration of Trypan Blue is known to give good results. Such treatments cannot be applied to dogs, cattle, or horses except in the case of very valuable animals. In general, it may be stated that the control of ticks is the most essential and effective method of keeping these diseases in check. However, the development of vaccines and serum treatments should prove of great value, and much progress may be looked for in these fields.

On domestic animals, as cattle, horses, dogs, etc., the most efficient method of destroying ticks is by dipping or spraying. The dip or spray employed is usually an arsenical one. Each country has its own official dip. That recommended by the United States Department of Agriculture is as follows:

Sodium bicarbonate	24 pounds
Arsenic trioxide (white arsenic)	8 pounds
Pine tar	1 gallon
Water	500 gallons

This material is prepared in a large dipping vat. The vat is so arranged that the cattle are driven into it one by one, swim through it, and walk out at the other end by means of an inclined, cleated plane. They are then held a short time in a dripping pen, the drip running back into the vat. By consistent periodic treatments large areas have been completely cleared of cattle ticks, as for instance most of the southern United States.

However, the problem of controlling such ticks as *Ornithodoros* spp., *Argas* spp., and those that normally attach only to wild animals is a much more

Table 5. A—Tick-borne human diseases. All these ticks have been proved to be vectors either in nature or by experimental evidence.

Disease and etiological agent	Tick vectors	Reservoirs	Method of trans-mission	Incubation period		Known distribution of disease
				In man	In tick	
1. Paralysis ?	*Dermacentor andersoni, D. variabilis, Ixodes holocyclus, I. pilosus, I. ricinus*	?	Bites	?	?	North America, Australia, Europe, India, South Africa
2. Relapsing fevers *Spirochaeta* spp.	See summary p. 72					
3. Rocky Mountain spotted fever *Rickettsia rickettsi*	*Dermacentor andersoni, D. parumapertus, D. variabilis, D. occidentalis, Amblyomma americanum, A. cajennense, Rhipicephalus sanguineus, Ornithodoros parkeri, O. nicollei, Haemaphysalis leporis-palustris*	Ticks, rodents, (squirrels, rabbits, etc.)	Bites	2–12 days		North America, South America (Brazil), Mexico
4. "Q" fever (Australian) *Rickettsia burneti*	*Ixodes holocyclus, Haemaphysalis humerosa*	Bandicoots (*Isodon* spp.), cattle	Feces or fecal wastes	?	?	Australia, Greece, Balkans, Italy, United States
5. "Q" or nine-mile fever (American) *Rickettsia diaporica*	*Dermacentor andersoni, D. occidentalis, Ornithodoros moubata, O. hermsi, Amblyomma americanum, Rhipicephalus sanguineus*	?	Bites, feces	?	?	United States (western), Panama
6. Boutonneuse fever *Rickettsia rickettsi conori*	*Rhipicephalus sanguineus*	Dogs, rats, wild rodents (?), *R. sanguineus*	Bites	?	?	Mediterranean area, North Africa
7. S. African tick-bite fever *Rickettsia rickettsi pijperi*	*Haemaphysalis leachi, Amblyomma hebraeum*	Vector ticks, dog	Bites	?	?	South Africa
8. Colorado tick fever ?	*Dermacentor andersoni*	?	Bites (?)	?	?	Colorado, Wyoming, Idaho

Table 5.—Continued.

Disease and etiological agent	Tick vectors	Reservoirs	Method of trans-mission	Incubation period		Known distribution of disease
				In man	In tick	
9. Bullis fever, Virus	*Amblyomma americanum*	?	Bites (?)	?	?	Texas (Camp Bullis)
10. Tick typhus ?	*Dermacentor nuttali,* other ticks?	Wild rodents (?), rats (?)	Bites (?)	?	?	Russia, India, East Africa (North America?)
11. Tularemia *Pasteurella tularensis*	*Dermacentor andersoni, D. parumapertus, D. variabilis, D. occidentalis, D. marginatus, Haemaphysalis leporispalustris*	Cottontail rabbits, other rodents, *Dermacentor* spp., *Haemaphysalis* sp.	Bites, contamination	3–5 days	?	North America, Europe (widespread), Turkey, Tunisia, Russia (Asiatic), Japan
12. Russian spring-summer encephalitis ?	*Ixodes persulcatus* *Dermacentor silvarum* *Haemaphysalis concinna, H. japonica; Ixodes ricinus*	Wild rodents (?)	Bites	?	?	Eastern Russia, Siberia, Urals, European Russia, Karelia
13. St. Louis encephalitis Virus	*Dermacentor variabilis*	Poultry, the tick, *D. variabilis*	Bites			Western United States

B—Other tick-borne diseases attacking animals.

14. Texas fever of cattle *Piroplasma bigemina*	*Boophilus annulatus, B. australis, B. microplus, B. decoloratus, Rhipicephalus evertsi, R. appendiculatus*	Ticks, recovered animals	Bites			North America, South America, West Indies, Africa, Australia
15. Red-water fever of cattle *Babesia bovis*	*Ixodes ricinus*	Ticks, recovered animals	Bites	?	?	Europe
16. Malignant jaundice of dogs *Babesia canis*	*Rhipicephalus sanguineus, Dermacentor reticulatus, Haemaphysalis leachi*	Ticks	Bites			South Africa, Europe, North America
17. "Carceag" of sheep *Babesia motasi*	*Rhipicephalus bursa*	*Rhipicephalus bursa*	Bites (adult)	?	?	Eastern and southeastern Europe

18. Horse piroplasmosis *Babesia caballi*	*Dermacentor reticulatus*	?				Southern and southeastern Europe, Caucasus
19. Biliary fever of horses *Babesia equi*	*Rhipicephalus evertsi* (in South Africa)	?				Southern Europe, Africa, southern Asia, South America
20. Heartwater of cattle, sheep, and goats *Rickettsia ruminantium*	*Amblyomma hebraeum*, *A. variegatum*	?				South Africa, French West Africa, Belgian Congo, Kenya, Tanganyika
21. Anaplasmosis of cattle *Anaplasma marginale*	*B. annulatus*, *B. microplus*, *B. decoloratus*, *Dermacentor andersoni*, *D. variabilis*, *D. occidentalis*, *D. albipictus*, *Hyalomma lusitanicum*, *Ixodes ricinus*, *I. scapularis*, *Rhipicephalus sanguineus*, *R. bursa*, *R. simus*	*B. annulatus*, *Dermacentor andersoni*, *D. occidentalis*, recovered animals	Bites			United States, South Africa
22. East Coast fever of cattle *Theileria parva*	*Rhipicephalus appendiculatus*, *R. evertsi*, *R. simus*, *Hyalomma* sp.		Bites			East coast of Africa, India, Transcaucasia
23. Nairobi sheep disease Virus	*Rhipicephalus appendiculatus*, *Amblyomma variegatum*, *Rhipicephalus neavei*	*R. appendiculatus*				British East Africa
24. Louping ill of sheep Virus	*Ixodes ricinus*		Bites	6–18 days		Great Britain, Russia (?)
25. Fowl spirochetosis *Spirochaeta gallinarum*	*Argas persicus*		Bites			South America, Egypt, Sudan, India, Australia, Germany
26. Equine encephalomyelitis Virus	*Dermacentor marginatus*	?	?			Eastern European Russia

difficult one. Many of these ticks are not known to act as vectors of disease-producing organisms, but others, as *Haemaphysalis leporis-palustris,* serve as agents in maintaining the natural reservoir. *Ornithodoros moubata,* which lives principally in and around human habitations, can probably be effectively controlled by proper housing and cleanliness. In the case of the two- or three-host ticks that live primarily on wild animals we have little knowledge or experience on which to base control measures. The only large-scale work carried on is that against *Dermacentor andersoni* in parts of Montana. Here the natural reservoir of the human disease, Rocky Mountain spotted fever, is the native rodents. The main efforts have been directed toward the destruction of the rodent hosts (squirrels, ground squirrels, rabbits, etc.) by means of poison baits and the killing of the adult ticks by the dipping of horses and cattle. By destroying the hosts of the larvae and nymphs it is hoped to starve out the ticks. Though this work has proved somewhat successful, it is difficult to see how it could be employed for many tick species. Recently a tick parasite, *Ixodiphagus caucurtei* du Buysson, was discovered in France and has been introduced into Montana and the eastern United States. The parasite is known to attack a number of different species of ticks. It is hoped that the employment of this parasite on a large scale may bring about a decided reduction in the disease-distributing species of ticks.

Personal prophylaxis must be relied on as the most effective means of avoiding tick-borne diseases. In tick-infested regions sleeping or sitting on the ground should be avoided, and camping places should be selected with care. The use of suspended hammocks for sleeping purposes is most essential. The clothing should be rather coarse and loose and the legs well protected by laced high boots or wrap puttees. Before entering dwellings or prepared camps for the night, all clothing should be carefully examined and adhering ticks destroyed. If convenient, a complete change of clothing is the wisest precaution. Each evening the clothing worn during the day should be carefully examined for adhering ticks. Only by careful attention can infestation by ticks be avoided. This is well illustrated in the case of *Dermacentor andersoni.* Though the most exacting precautions have been observed in the tick-control work in Montana, yet at least five men have died through contracting the disease in some unknown manner.

Since the discovery of the effectiveness of various DDT combinations in controlling mosquitoes, lice, fleas, and other insects, experiments have been conducted with this material against ticks. Areas infested with various species of ticks have been sprayed, but the results are not very gratifying. A certain amount of control is indicated with such species as *Dermacentor variabilis* and *Amblyomma americanum*. Fair control of *Rhipicephalus sanguineus* has been obtained when 10 per cent DDT dusts have been applied in houses. In all probability some effective agent against ticks may be developed. No satisfactory repellent has been developed.

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CHAPTER IV

The Order Acarina; Parasitoidea, Sarcoptoidea, Trombidoidea, Tarsonemoidea, Tyroglyphoidea, and Demodicoidea

THE PARASITOIDEA

THE Parasitoidea contain at least three rather large families. Their structure allies them with the ticks. Tracheae are present and open through a pair of spiracles located on spiracular plates placed usually above and between the third and fourth coxae. The mouth parts are well developed and consist of chelate or piercing chelicerae, an unarmed hypostome, and a pair of small palpi. The ventral surface lacks furrows, but sclerotized plates are generally present. Only one family, the Dermanyssidae, is of interest here. The members of this family may be recognized as they are all true parasites of reptiles, birds, and mammals. The chelicerae are needlelike or shearlike, usually without teeth. Ventral and anal plates are nearly always present and separate; a dorsal plate is present but covers only a part of the body. Only two genera of this large family are known to contain species that may attack man or be found associated with the transmission of disease. These two genera may be separated by the following couplet:

1. Chelicerae shearlike, both arms present (Fig. 26) .... *Liponyssus*[1]
2. Chelicerae needlelike and long (Fig. 26) .... *Dermanyssus*

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[1] This genus and a number of related genera were separated by Ewing (1923) and placed in a subfamily, Liponyssinae; later Vitzthum (1931) created the family Liponyssidae for these genera; recently da Fonseca (1948) changed the family name to Macronyssidae.

Dermanyssus gallinae (Linn.) is the common chicken mite (Fig. 27). It is bloodsucking in habit and usually feeds at night when the fowls are roosting. The mites engorge rapidly and leave their hosts to spend the day hidden away in cracks, crevices, and trash about poultry houses. The eggs are laid in the trash and rubbish; they hatch in three to four days. The larval and nymphal life occupies ten days to two weeks. The mites will attack persons handling infested fowls or sleeping in or near infested poultry houses. Though the mites cause a marked dermatitis in humans, it is said they do not obtain human blood. Avoidance of the mites is all that is necessary to reduce the dermatitis as they do not live long on the human body. Recently it has been shown by Smith *et al.* (1944, 1945, 1946) that the chicken mite appears to be the natural transmitter and reservoir of the St. Louis encephalitis virus among chickens. Furthermore these workers demonstrated that the virus is passed through the eggs to the offspring of the mites. As chickens are also reservoirs of this virus and as *Culex pipiens* (the common house mosquito) is a common feeder on chickens and on man, it is well established that this mosquito is an important vector of this disease to man. Here we have the complex of the chicken mite maintaining the virus in chickens and the mosquito (*Culex pipiens*) transferring the virus to man. The mosquito may also serve as a

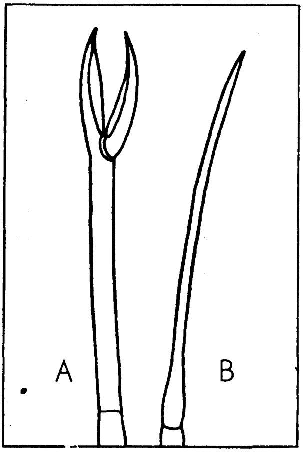

Fig. 26. (*A*) Chelicera of *Liponyssus bacoti.* (*B*) Chelicera of *Dermanyssus gallinae.*

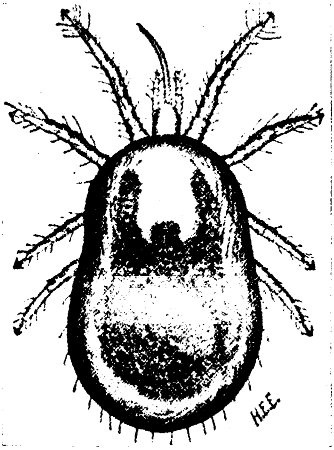

Fig. 27. Dermanyssus gallinae, the chicken mite. Dorsal view. (After Ewing.)

vector from chicken to chicken. An adequate control of the chicken mite might aid in the reduction of the incidence of this disease among men. Howitt *et al.* (1948) recovered the virus of eastern equine encephalomyelitis from *Dermanyssus gallinae* taken in nature in Tennessee; they also isolated the virus in the chicken lice, *Menopon pallidum* Nitsch. and *Eomenacanthus stramineus* (Nitsch.) taken from poultry. This is the first recovery of this virus from insects in nature.

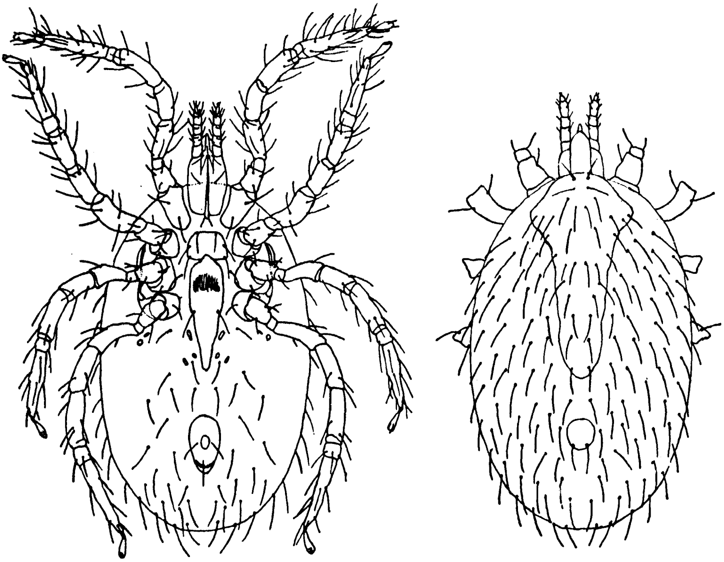

Fig. 28. Dermanyssus (*Allodermanyssus*) *sanguineus. Left:* Ventral view of female. *Right:* Dorsal view of female. (Redrawn and modified from Hirst.)

Dermanyssus (*Allodermanyssus*) *sanguineus* Hirst is a parasitic mite on rats and mice. It was described from Egypt in 1914. The female can be easily separated from *D. gallinae* by the possession of two dorsal shields, the posterior one being small and circular (Fig. 28). *D. sanguineus* was first reported from America in 1923 by Ewing, though collected in Washington in 1909. At present it is known from New York, Philadelphia, Boston, Indianapolis, and Tucson as well as from Washington, D.C. In 1946 a peculiar febrile disease of unknown etiology appeared in parts of New York City. Huebner *et al.* (1946) reported this disease (Rickettsialpox) as due to a rickettsia, which he named

Rickettsia akari. This rickettsia was recovered from the mite and from patients suffering from the disease; mice were infected by mites carrying the rickettsia. During the summer of 1946 over 100 cases of human infection were reported from New York City.

Liponyssus bursa (Berlese) and *Liponyssus sylviarum* Canestrini and Fanzago are mites that commonly infest poultry, and man may be attacked when handling infested birds. *L. bacoti* (Hirst) is frequently called the tropical rat mite (Fig. 29) as it was originally described from Egypt and was thought to be mainly distributed in tropical countries. It is now known to be widely distributed in many parts of the world including the United States. In America it is known from many states and occurs at least as far north as New York and Minnesota. This mite is primarily a parasite of rats, but it readily attacks man, especially in such places as buildings, granaries, storehouses, public buildings, stores, or even private homes where rats are abundant. The mite feeds only on blood. The nymphs and adults drop from their hosts after each blood meal; thus the mite may feed on a variety of different animals during its life cycle. This feeding habit is well adapted to the transmission of a blood virus or parasite. The life cycle is comparatively short. The eggs hatch in about four days and the adult stage may be attained 12 days later. Dove and Shelmire found that at least four blood meals are necessary to rear a larva to

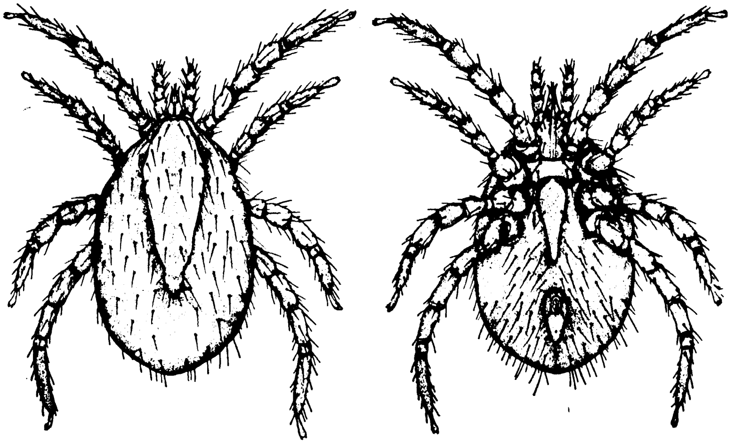

Fig. 29. Liponyssus bacoti, the tropical rat mite. Dorsal and ventral views. (After Dove and Shelmire, *Journal of Parasitology.*)

the adult stage. The only known way to control the mites is to destroy the rats. DDT might prove an effective control method in rat-infested buildings where killing of the rats is not feasible.

Shelmire and Dove (1931) described a large number of cases of dermatitis caused by this mite. The eruptions appeared as urticarial wheals varying in size from that of a pinhead to that of a split pea. On children urticarial welts, papules, and vesicles are often present. Severe pruitus may result, and secondary infections may occur from scratching. The author has received several reports of severe infestations of this mite in large manufacturing plants in New York state. The mites gradually disappeared with the destruction of the rats.

The above authors also proved experimentally, with rats and guinea pigs, that this mite can transmit endemic (murine) typhus. They showed that the infection in mites is transmitted to their offspring, the young larvae from infected mothers producing typical murine typhus in guinea pigs by their bites. Later they demonstrated that the mite is capable of maintaining the infection in wild rats and concluded that rats are important reservoirs of murine typhus, a fact that is now well known.

Philip and Hughes (1948) have demonstrated that this mite can transmit experimentally rickettsialpox (*Rickettsia akari*) and have presented data that indicate transovarial transmission of the parasite.

THE SARCOPTOIDEA

This superfamily is restricted to atracheate mites, parasitic on animals, mainly birds, mammals, and insects. Many of the external structures generally found in mites are greatly reduced or lacking. The mouth parts are modified and reduced so that the parts cannot be distinguished easily (Fig. 30). The palpi, so prominent in the ticks, are almost lacking in segmentation and are often more or less fused with the mouth parts. The chelicerae are reduced to mere sclerotized rods or blades; a hypostome is lacking. The skin of the body is marked with fine parallel folds, and it bears, especially on the dorsal surface, minute setae, stout spines, and cones or modifications of them. The legs are short and frequently modified for clasping. Usually the legs, or some of them, terminate in a stalked sucker or long hair. The two anterior pairs are widely separated from the two posterior pairs.

The sarcoptoid mites live on their hosts throughout their life, mating and egg laying taking place on their hosts. They infest the skin, tissues, hairs, or feathers of their hosts. Sexual dimorphism is usually marked, the males possessing special structures for clasping or holding the females. The principal families may be separated by the following key (adapted from Banks and Ewing):

KEY TO FAMILIES OF SARCOPTOIDEA

1. With special apparatus for clinging to hairs, usually either modified legs or chelicerae. Parasitic on mammals. (Contains no species of known medical importance) .... *Listrophoridae*
   No such special clinging apparatus 2

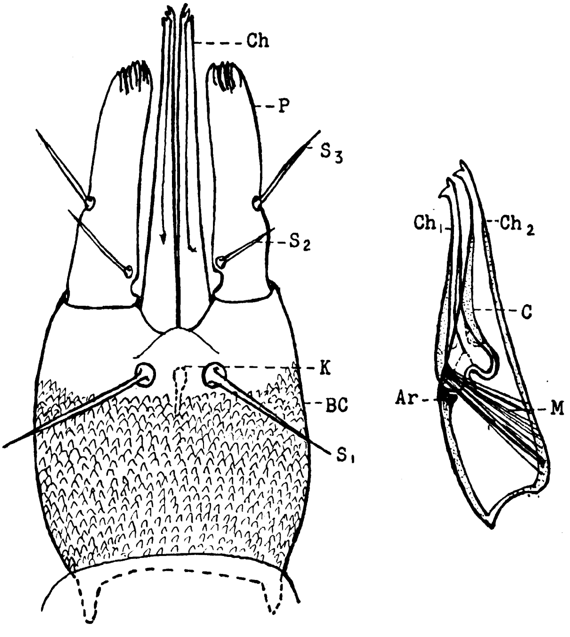

Fig. 30. Left: Dorsal view of capitulum of *Psoroptes communis* var. *cuniculi. Right:* A single chelicera, greatly enlarged. Ar, articulation of internal part of chelicera; BC, basis capitulum; C, Ch_1, Ch_2, chelicerae; M, the muscle; K, a keellike structure on basis capitulum; P, palpus; S_1, S_2, S_3, spines.

2. Bird-infesting mites, living on or among the feathers; usually heavily sclerotized .... *Analgesidae*
   Mites not living on or among the feathers of birds; soft-bodied mites 3
3. Parasitic on insects only .... *Canestriniidae*

Parasitic in or on the living tissues of vertebrates 4

4. Vulva longitudinal; parasitic in the skin and tissues of birds (mainly the air passages and air cells) . . . . *Cytoleichidae*

Vulva transverse; parasitic in or on the skin of mammals and birds . . . . *Sarcoptidae*

THE FAMILY SARCOPTIDAE

Species of this family produce skin diseases of man and other animals known under such names as scabies, sarcoptic itch, "Norwegian itch," "barber's itch," psoroptic itch, acariasis, etc. The species are all skin-infesting and live primarily beneath the scabby incrustations that their activities induce. Certain species (*Sarcoptes* spp.) are burrowing in their habit and form tunnels below the surface of the skin. Though a considerable number of genera have been described in this family only a few of them are of interest here. These may be separated by the following key.

KEY TO GENERA OF SARCOPTIDAE

1. Suckers of the tarsi with segmented pedicels; males with anal suckers (Fig. 32 *A*) . . . . *Psoroptes*

Pedicels of the suckers not segmented or suckers may be absent (Fig. 31 s) 2

2. Females with tarsal suckers lacking on all the legs; anal opening terminal; parasitic on birds . . . . *Cnemidocoptes*

Females with tarsal suckers on some of the legs 3

3. Tarsal suckers on all the legs of the male and on the first, second, and fourth of the female. (Species infest horses and cattle) . . . . . . *Chorioptes*

Tarsal suckers not arranged as above; suckers on the first, second, and fourth pairs of legs of the male; on the first and second pairs of the female (Fig. 31 *B*) 4

4. Anal opening on the dorsal surface; dorsal surface of the body with only short, sharp setae . . . . *Notoedres*

Anal opening terminal or partially ventral; dorsal surface of the body with pointed scales and blunt, stout spines (Fig. 31 *A*) . . . . *Sarcoptes*

THE GENUS *SARCOPTES* LATREILLE 1806: *Sarcoptes* contains those species that produce the true scabies or itch of man and animals. Whether there is only one species with numerous varieties or a number of distinct species attacking different animals is still a much-disputed question. Furthermore, whether the various so-called species on different animals will attack man has not been determined for many of them. It is preferable to follow the practice of recognizing only one valid species and listing as varieties or subspecies those found on different animals. The type species is *Sarcoptes scabiei* de Geer, found on man, though it is often written *S. scabiei* var. *hominis* (Hering).

Sarcoptes scabiei: The human itch mite has been carefully studied by several workers, especially in recent years. The adult female (Fig. 31) measures 330 to 450 microns in length and 250 to 350 microns in width. The male is considerably smaller, a little more than half the size of the female. The dorsal surface of the body is marked with numerous parallel lines except in an anterior median area; stout, blunt spines and irregular scales are present and arranged as shown in Fig. 31. Several pairs of long and short hairs are also present. The number, arrangement, length, and shape of these structures seem to be of some systematic significance. The ventral surface is smooth except for

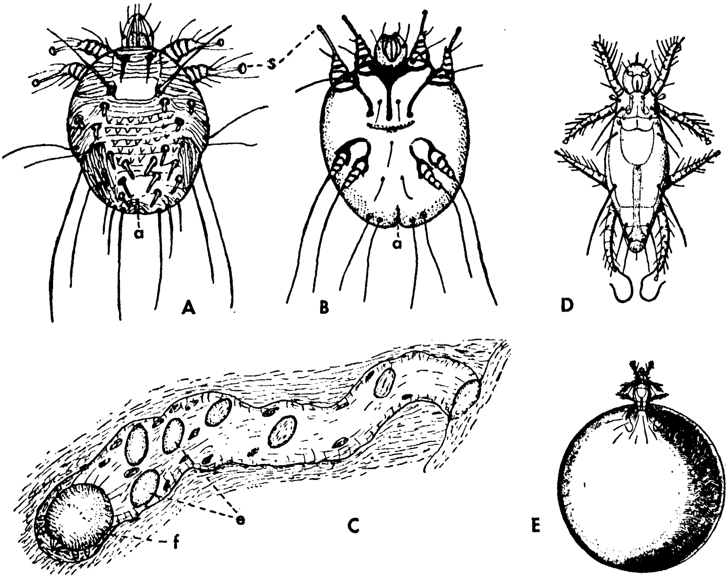

Fig. 31. (*A*) and (*B*) Dorsal and ventral views of *Sarcoptes scabiei.* (*C*) *Sarcoptes scabiei* in its burrow in the skin. (*D*) *Pediculoides ventricosus,* mature female before the development of its young. (*E*) *P. ventricosus,* female, showing the abdomen greatly swollen by the developing young (*D* and *E* not drawn to the same scale). a, anal opening; e, eggs in burrow; f, female at end of burrow; s, suckers.

a few hairs or bristles. The anterior two pairs of legs are widely separated from the posterior two pairs. The most striking structures are the epimeres or chitinous supports for the legs (Fig. 31 *B*). The epimeres of the first pair of legs are united and form a narrow rod lying in the median line; those of the second pair do not unite but lie on either side of the body. The epimeres of the last two pairs of legs are not so prominent except in the male where they unite. The tarsal suckers consist of unsegmented pedicels and are present on the first and second pairs of legs of the female and on the first, second, and fourth of the male.

LIFE CYCLE: This mite and its various subspecies excavate horizontal, tortuous tunnels in the upper epidermis, the horny layer (Fig. 31). In man these burrows are usually found on definite areas of the body, particularly between the fingers, wrists, elbows, axillae, region of the groin and external genital organs, back of the knees, ankles, and toes. In children all parts of the body may be infested; in women the undersides of the breasts are said to be favorite locations. According to Munro definite egg burrows are made by the mature female. She bores directly into the skin, becoming completely concealed in from a few minutes to nearly an hour. Burrowing usually continues, and 2 to 5 mm. is excavated daily. Egg laying commences with the burrowing and continues for about four to five weeks. The eggs are deposited directly behind the female (Fig. 31), and normally she deposits one or two eggs each day. The exact number of eggs laid by a single female has not been determined but probably 40 to 50 is about the average. The eggs hatch in from three to four days. The larvae leave the parent burrow and, passing to the surface of the skin, enter hair follicles or penetrate the skin between hairs; vesicles may form. The larval stage lasts from two to three days. The larva then molts in its burrow. There are two nymphal stages, the nymphs making narrow, shallow burrows. Mating takes place in the burrows, the males seeking out the females, though Mellanby (1943) thinks mating occurs on the surface of the skin. The fertilized female then proceeds to form an ovigerous burrow. The entire life cycle from egg to adult varies from 8 to 15 days. The adults live for three to five weeks. As the life cycle is comparatively brief, a mild infection may become marked in a short time. According to Mellanby, it requires several weeks before an infection becomes apparent and requires medical attention. He has also shown that in man (some 900 cases) the average number of adult female mites per patient rarely exceeds fifty. However, many severe infestations have been reported, and the number of mites must have been large or secondary infection (bacterial) occurred.

EFFECT ON HOST: The initial attack is without definite symptoms for the first few weeks. As the host becomes sensitized, the presence of the mites in the skin causes intense itching, especially at night when the warmth induces the mites to greater activity. Incessant scratching follows, and the effects of the scratching may be more serious than the work of the mites. Where the egg channels are formed and the larvae and nymphs burrow in the skin, small serous vesicles appear. Scratching ruptures these vesicles, and, on healing, minute crusts are formed. In severe infestations secondary complications may follow, such as infection with *Streptococcus* species. Diagnosis of scabies must rest on finding the mites and the burrows in the skin. The mites are not present in the vesicles but usually close beside them at the end of linear, shallow burrows. As scabies may be masked or confounded with other skin diseases, it is essential that the mite be found before a final diagnosis is made.

Sarcoptic mites are not easily transferred by simple contact, though cases of such are on record. The most common methods are by close contact with infected persons, as by sleeping with them, by cohabitation, by using their clothing or bedding, or, among children, by playing and holding hands. Munro has shown that the cast-off clothing of infected persons remains capable of infecting others for at least 11 days if the clothing is moist; if the clothing is dry, infection dies out in two or three days. During the First and Second World Wars there were severe outbreaks of sarcoptic itch in the various armies. These outbreaks, though marked among the troops, were also present in the general population of many countries. Mellanby (1943) states that in Great Britain the normal population showed an infection rate of about 1 per cent in 1939 and this increased to about 5 per cent in many parts of the country during the war. The average for the country as a whole was about 2 per cent. Women, especially young women, showed an incidence about twice as great as did males.

TREATMENT: Persons infected with sarcoptic itch should obtain medical attention. During the last world war several effective treatments were developed, and these proved easy of application. The American Army formula was known under the code name NBIN and consisted of the following compounds: benzyl benzoate 68 per cent; DDT 6 per cent; benzocaine 12 per cent; Tween 80, 14 per cent (all by weight). For treatment the concentrate should be diluted at the rate of one part to five parts of water. Before applying treatment the infected person should take a hot bath, scrubbing the lesions vigorously with a tincture of green soap. The dilution may then be applied either by a sponge or as a spray, and the whole body should be carefully covered. The patient should not bathe for at least 24 hours. Many reliable proprietary brands are on the market as benzyl benzoate solutions, benzyl benzoate ointment, or other trade names. These are said to be very effective, and the patient should follow the directions of the manufacturer. One thorough treatment by these preparations usually gives complete cure, though it may be well to follow this by a second about a week later. The British formula as given by Mellanby (1943) is very easy to prepare and is said to be very easy on patients with tender and abraded skins. It is as follows: "Benzyl benzoate, 200 mils; Stearic acid, 20 gr.; Triethanolamine, 6 mils; water to produce 1000 mils. Heat the benzyl benzoate and stearic acid together until the latter is dissolved. Mix the triethanolamine with the water and then pour into the warm benzyl benzoate acid mixture and stir." This makes a good emulsion and is very easy on the skin. Other mixtures are also on the market but those with benzyl benzoate as the prime ingredient are preferred. Where these compounds cannot be obtained the sulphur ointment (10 to 15 per cent) may be used, but this requires at least three treatments morning and evening without bathing. Bathing should precede the first treatment and follow the last. In all cases the clothing and bedding of infected patients should be sterilized by laundering or by dry heat.

The so-called "Norwegian itch" is caused by the same species of *Sarcoptes* but oftentimes is marked by gigantic crusts due to long infestations. Another disease called "craw-craw" in parts of Africa is characterized by nodular and scabby dermatitis but has been shown to be caused by *Sarcoptes.*

Other Sarcoptes: Itch mites have been described from many different mammalian hosts. Over 18 to 20 different species or varieties are known, as *S. equi* (from the horse), *S. canis* (from the dog), *S. ovis* (from the sheep), *S. suis* (from the pig), and *S. bovis* (from the ox). Nearly all recent work indicates that these are not separable on morphological characters but appear as physiological races or varieties of the one species *S. scabiei* de Geer. If this is true, can man become infected by the animal-infesting forms? There are many records of man's becoming infected with some of these forms, especially by *S. scabiei* var. *equi* (by grooms and others attending infested horses), by var. *caprae* and var. *ovis* (by goat and sheep herders). During a recent epidemic of scabies of cattle by *S. scabiei* var. *bovis* in the northeastern United States there were many reports of human infection, but so far as the writer is aware these infestations were of a temporary nature.

THE GENUS *PSOROPTES* GERVAIS 1841: Species of *Psoroptes* are nonburrowing itch mites that possess tarsal suckers with jointed pedicels

(Fig. 32). Like *Sarcoptes,* rather numerous species of *Psoroptes* have been described from various animals. *P. communis* var. *ovis* (Hering) produces a serious disease of sheep, psoroptic itch or scab. The mite causes the wool to fall out or to mat together and severe scabby incrustations to form, and, in general, the infected animals present a scraggy and dilapidated appearance. This disease is widespread in sheep-raising regions but can be controlled by the use of appropriate dipping solutions. Other varieties are *P. communis* var. *equi,* on horses; var. *bovis,* on cattle; var. *cuniculi* (Fig. 32), on rabbits. (This variety on rabbits seems to prefer the ears and, in laboratory animals, causes them to swell enormously. Frequently they penetrate deeply into the ear and cause death.) Many other varieties from different animals have been recognized.

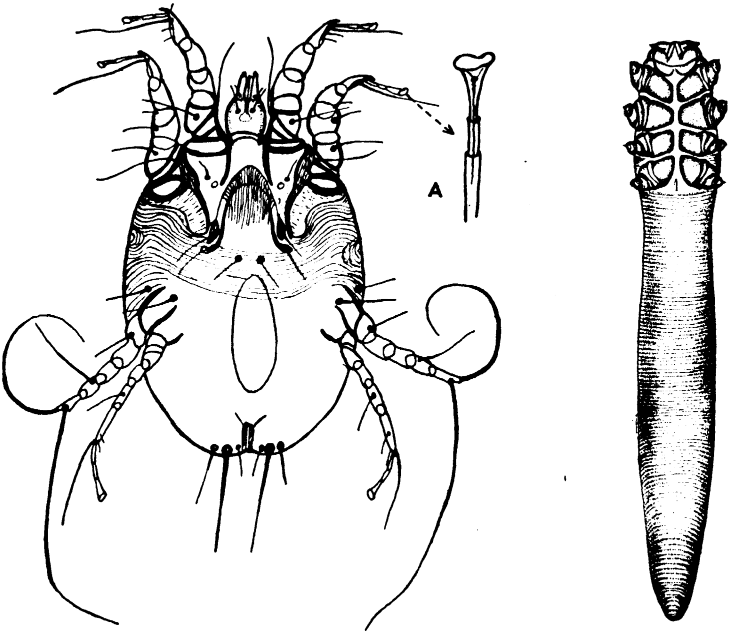

Fig. 32. Left: A common nonburrowing itch mite, *Psoroptes communis. Right:* A hair-follicle mite, *Demodex folliculorum.* A, segmented pedicel of sucker.

OTHER GENERA: Species of the genus *Notoedres* infest cats and rats. They are found principally about the ears, snout, tail, and anogenital region or among the fine hairs of the lower part of the legs. The itch produced is rather severe. The species on cats or rats may also occur on man. Gordon *et al.* (1943) give an extended account of the habits and biology of this mite. *Chorioptes equi* causes a mange on the feet of horses and *C. bovis* produces a mange on cattle. *Cnemidocoptes mutans* affects fowls, causing a rather serious disease known as scaly leg; *C. gallinae* is found at the base of feathers and is known as the "depluming mite."

THE TROMBIDOIDEA

The Trombidoidea constitute a large group of mites that are mainly free-living, feeding on plant juices, or they are predaceous; some are parasitic while others are free-living in the nymphal and adult stages and parasitic in the larval stage. They are tracheate mites, the spiracles located on or near the bases of the chelicerae. The mouth parts are either prominent and raptorial or they are modified for piercing and sucking. The last segment of the palpus is modified into a thumblike structure capable of apposing the clawlike extension of the penultimate segment. The body is never strongly sclerotized, and chitinous plates are rarely present.

This group is divided into a number of families, six or more. Only one family, the Trombidiidae, is of interest here as it contains species that are frequently parasitic in the larval stages, on man and other animals. Parasitic forms are known in some of the other families and a few have been reported as annoying to man, but they are of minor importance. This family is frequently divided into two subfamilies, the Trombidiinae and the Trombiculinae. Recently Ewing (1944) has recognized these as distinct families. They may be separated by the following brief key:

1. Abdomen of adults and nymphs strongly constricted somewhat in front of the middle; eyes, when present, never stalked. Eggs laid singly. Larvae parasitic on vertebrates .... *Trombiculinae*
2. Abdomen of adults and nymphs not constricted; eyes usually present and frequently stalked. Eggs laid in clusters. Larvae parasitic on invertebrates .... *Trombidiinae*

THE SUBFAMILY TROMBICULINAE

To this subfamily belong the harvest mites, the chigger mites, and others that are parasitic on vertebrates during their larval stage and are free-living in the nymphal and adult stages. Many of these mites are brilliantly colored—red, scarlet, or spotted with variegated colors. They bear various names as "chiggers," "harvest mites," "scrub mites," *bête rouge,* and *rouget.* Until recently only a few genera were known, but at the present time some 26 genera and a large number of species have been described; many or most of them are from the Oriental and Australasian regions. Michener (1946) states that 13 genera are known from the Western hemisphere, and these include about 90 species. Of these 90 species only 8 are known as adults or have been reared to the adult stage. The species are based mainly on the larval state since very few (10 species) have been reared to the adult stage. The following species are of interest because of their constant attacks on man or as vectors of important diseases.

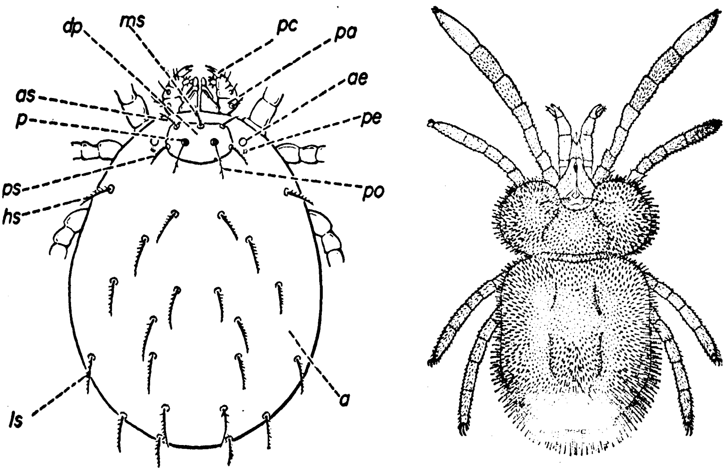

Fig. 33. Eutrombicula alfreddugesii (Oudemans). *Left:* Larva (North American chigger), greatly enlarged. *Right:* Adult. a, abdomen; ae, anterior eye; as, anterolateral seta; dp, dorsal plate; hs, humeral seta; ls, lateral seta; ms, median seta; p, pseudostigma; pa, palpus, pc, palpal claw; pe, posterior eye; po, pseudostigmatic organ; ps, posterolateral seta. (From *Manual of Tropical Medicine,* courtesy W. B. Saunders; modified from Ewing.)

Eutrombicula alfreddugesii (Oudemans) [*Leptus irritans* of literature] is the common chigger (Fig. 33) that attacks man in North America. It is generally distributed from New York to Minnesota, southward to the Gulf of Mexico and in Mexico. In the southern states it is very prevalent during the summer months, and its attacks are very annoying. The larval mites are very minute and easily penetrate the clothing. They attach by means of their hooked chelicerae and armed palpi. The method of feeding is very interesting. The chelicerae are inserted in the skin, frequently about a hair follicle and usually under or near clothing where there is pressure. The mite then injects into the tissues a fluid that has a remarkable effect. This fluid liquefies the immediate tissues, but the surrounding tissues become hardened and form a tube, frequently referred to as the stylostome or hypostome (Fig. 34). The liquefied tissues are ingested by the mite, and as feeding continues the tube becomes lengthened as more of the tissues are dissolved. The stylostome may become as long as the mite, and when the mite releases its hold this tube is left in the tissues. The effect of the digestive juices is to cause severe itching followed by a marked dermatitis. Incessant scratching may bring about secondary infection, and the result may be dangerous. After feeding, the larval mites drop to the ground and later molt to the eight-legged nymphal stage. The nymphs are not parasitic and probably feed on vegetable matter. This is also true of the adults. The females deposit their eggs singly on the ground. How many generations develop in a summer season does not seem to be known. In the larval stage this mite attacks all sorts of vertebrates as rabbits, mice, rats, snakes, turtles, poultry, and quail. Jenkins (1947) gives a concise account of rearing several generations of this mite and also of *E. masoni*. He reared the nymphs in soil in jars, feeding them on the eggs of mosquitoes (*Aedes aegypti*). At the present time this mite is not known to transmit any human disease.

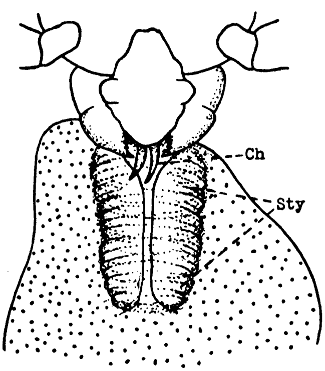

Fig. 34. A diagrammatic illustration of the formation of the stylostome by a *Neoschongastia* sp. in the ear of a rat. Ch, chelicerae of mite; Sty, stylostome.

Eutrombicula batatas (Linn.), known as the "patatta" mite of Surinam, occurs from Surinam to Panama, north to Puerto Rico, Florida, Alabama, and parts of Mexico. According to Michener (1946), the adults are found in open sunlight areas among short grass. The females lay their eggs on the ground. The eggs hatch in four to five days into what has been called the "deutovum" stage of mites (the eggshell bursting and showing a quiescent undeveloped larva, Fig. 35). This stage lasts six to seven days, and from it emerges an active, six-legged, reddish larva. The larvae occur on the grass or weeds, often in great numbers, especially about houses where domestic animals such as chickens are numerous. The larvae readily attach to man, domestic animals, rats, or birds. On man they seem to settle mostly in the

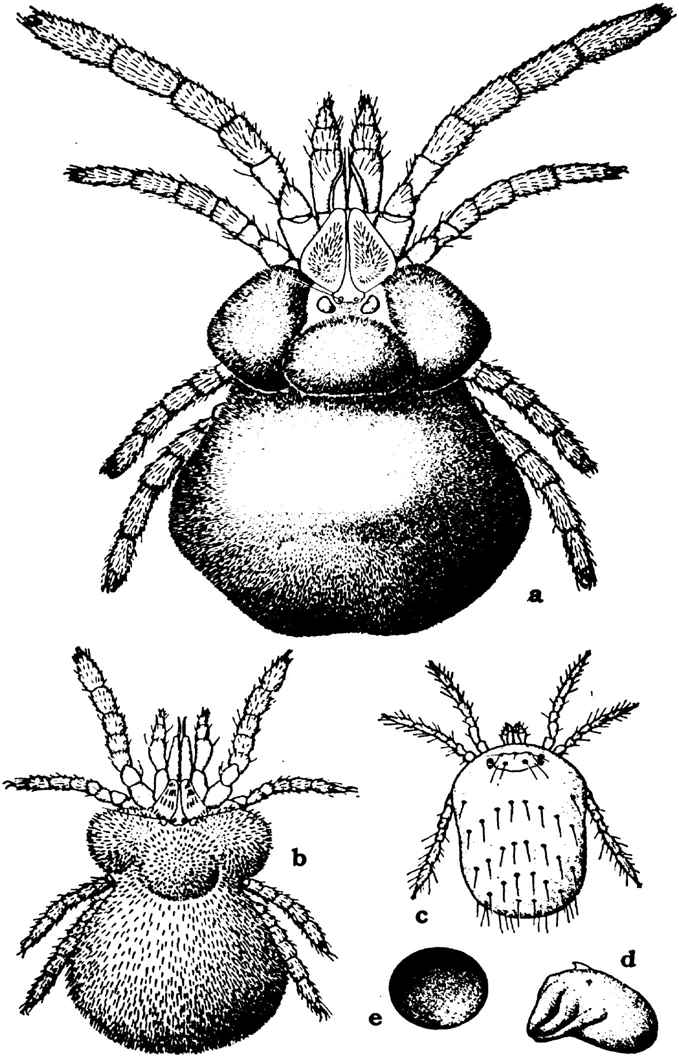

Fig. 35. A chigger mite, ***Eutrombicula batatas*** (Linn.). (*a*) Dorsal view of adult. (*b*) Dorsal view of nymph. (*c*) Dorsal view of larva. (*d*) Lateral view of deutovum. (*e*) The egg. (All to the same scale; after Michener, ***Annals of the Entomological Society of America.***)

groin region, under the armpits, under the belt line, or on the ankles under the socks. They remain attached for three to six days and then drop from their hosts. Within the larval skin the protonymph appears, and later the first nymphal stage emerges from the larval and protonymph integuments in six or seven days after the larva dropped from its host. The eight-legged, dull-red nymph looks like the adult except in size. The nymphs remain on the ground, but their exact food was not determined. In about two weeks or longer the nymphs become quiescent and in about a week transform to adults. The adults have been kept alive for at least 45 days. Though the exact food of the nymphs and adults was not determined, Michener suggests that they live on the soil moisture rich in organic matter as they possess sucking mouth parts. This species is not known to transmit any disease.

Trombicula autumnalis (Shaw) is a very troublesome mite in various parts of Europe. It is a pest not only of man but of horses, cattle, dogs, cats, and rabbits. According to Fuss and Hansen (1933), it produces on man a severe dermatitis with inflammation, necrosis of the epidermis, and hyperemia. The itching is intense.

Trombicula akamushi (Brumpt) occurs over extensive areas of Japan, Formosa, parts of Korea, and the Pescadores, and it is reported from the Malay Peninsula. This species is of great importance as it is known to be the vector of Japanese river fever, tsutsugamushi disease, or, as it is frequently called, kedani fever. The life history of this mite and its relation to tsutsugamushi disease were rather fully elaborated by Japanese workers between 1900 and 1918. In World War II tsutsugamushi disease appeared among American and Allied troops in various parts of the South Pacific and Burma theaters of operations. As a result extensive and intensive investigations have been carried on and much new data obtained.

T. akamushi (Fig. 36), like other mites parasitic in the larval stage, not only feeds on man but attacks mice, rats, and other rodents. It is especially fond of the voles (*Microtus montebelli* in Japan) in the ears of which it seems to congregate. The period of larval attachment is three to four days. The method of feeding is similar to that of *Eutrombicula alfreddugesii.* (This is believed to be true of all the parasitic larval mites of the subfamily Trombiculinae.) Leaving the host the larvae seek shelter in the ground, where they transform to nymphs in from two to three weeks. The nymphs are said to feed only on plant juices or decaying organic matter. The nymphal period lasts some three to ten or more weeks (no very accurate data seem to be available on the activities and length of the nymphal life). The adults live on the ground and are said to feed on plant juices. They are known to hibernate during the winter in Japan. In the spring the females deposit their eggs singly on the ground under trash or other covering. Unfortunately very few new data have been obtained on the life cycles, habits, or biology of the various species of mites occurring in the regions where kedani fever is now known to be prevalent.

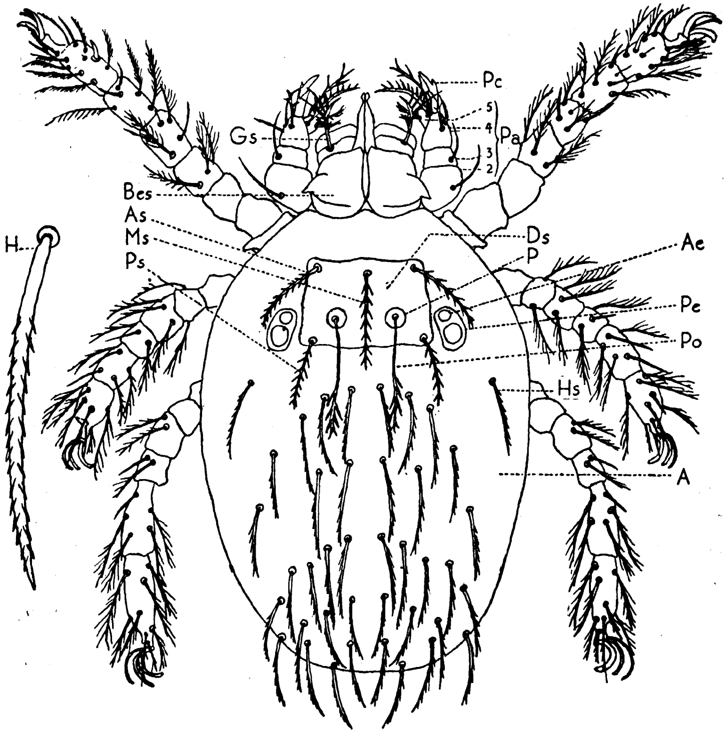

Fig. 36. Larva of *Trombicula akamushi.* A, abdomen; Ae, anterior eye; As, anterolateral seta; Bes, basal segment of chelicera; Ds, dorsal shield or plate; Gs, branched galeal seta; H, one of the dorsal hairs; Hs, humeral seta; Ms, median seta; P, pseudostigma; Pa, palpus; Pc, palpal claw; Pe, posterior eye; Po, pseudostigmatic organ; Ps, posterolateral seta. (Modified from Hirst.)

Trombicula deliensis Walch was described from Sumatra. It is distributed in many parts of Malaya, northern India (Simla Hills), the East Indies, northern Australia, and probably in other parts of southeastern Asia. It occurs on various species of rats and other rodents and readily attacks man.

Trombicula fletcheri Womersley and Heaslip was described in 1943. It is found commonly in the New Guinea area and readily attacks man. It is a common parasite of rats and bandicoots and is recorded from several other hosts. Little seems to be known of its life history, and its distribution is, as yet, not fully known. *Trombicula walchi* was described by Womersley and Heaslip from the New Guinea area, but many authorities seem to think it is the same as *T. deliensis.*

Many other species of *Trombicula* and related genera have been described from the southwest Pacific area, but little is known about their biology or distribution. *Trombicula hirsti* Sambon is generally called the "scrub mite" of parts of Australia; *T. wichmanni* Oudemans, is said to be a pest in the Celebes and New Guinea; *Leeuwenhoekia australiensis* Hirst is troublesome in New South Wales.

CONTROL OF MITES: Very effective mite repellents were developed during the recent world war. Briefly these are:

(1) Dimethyl phthalate or dibutyl phthalate used as liquids on all openings of the clothing. These are applied by hand or the entire clothing can be sprayed. In using them apply liberally along all openings and especially about the socks and edges of trousers. These materials can also be used to impregnate clothing. These solutions can be purchased and the directions of the manufacturer should be followed.

(2) Benzyl benzoate as developed in the NBIN formula for the control of sarcoptic itch mites is also effective (see pp. 103–104). Clothing is impregnated with this mixture and it withstands several launderings or even longer.

(3) Benzyl benzoate alone also gives excellent repellent effect when clothing is impregnated with it. The repellent effect persists even after four or five launderings.

(4) Other repellents have been tested but not sufficiently to warrant their use at the present time.

TROMBICULID MITES AND DISEASE: The attacks of various species of mites throughout the world usually result, in man, in a marked dermatitis accompanied by intense itching. The scratching of the areas may induce secondary infections that may be serious. However, it is as vectors of disease that certain species are dangerous.

Tsutsugamushi disease was recognized in man in Japan as early as 1878, and Baelz and Kawakami (1879) published on account of what they described as "Japanese river fever." The disease was confined to overflow areas of certain river valleys. The natives associated it with the bite of a red mite (akamushi). Japanese workers, between 1893 and 1918, fully established that the mite, *Trombicula akamushi,* was the vector of the disease; that rodents, principally the vole, *Microtus montebelli,* were the reservoir; and that the virus is passed through the egg to the young of the infected mites. They also described the life cycle of the mite and largely determined its distribution in Japan and Formosa. In 1930 Nagayo and his associates discovered the etiological agent and named it *Rickettsia orientalis.* It is now well established that the reservoir of this disease is in rats, mice, voles, and other rodents; the mites obtain the rickettsiae while feeding on infected hosts, and these are passed through the nymphal stage to the adults and by the adults through the eggs. Larvae from infected mothers then transmit the disease to man when they feed on him. The point of feeding by infected larvae usually shows a distinct scar (eschar). The incubation period in man is 7 to 10 days or may be prolonged to 14 days. The mortality rates vary, but range from 60 per cent for older persons to 15 per cent for the 11- to 20-year age group in Japan. Blake *et al.* (1946) give an over-all death rate of 30 per cent in Japan. Throughout southeast Asia, the islands of the southwest Pacific, and Australia various typhuslike diseases have been described such as Mossman fever from Australia, scrub typhus from Malaya, pseudotyphus from Sumatra, endemic typhus from India, and tropical typhus from Indo-China. During World War II these diseases were investigated by a large number of workers with the result that all these diseases were declared to be manifestations of tsutsugamushi disease. At present this disease occurs in India, Ceylon, Burma, Indo-China, Malaya, Sumatra, Java, Borneo, Celebes, New Guinea, northeast Australia, New Britain, Bougainville, parts of the Philippines, Formosa, Japan, Korea, and probably parts of China. The vectors are *Trombicula akamushi, T. deliensis, T. fletcheri, T. walchi* (= *deliensis*), and probably others. The reservoirs of *Rickettsia orientalis* are in voles (especially *Microtus montebelli* in Japan), in wild rats of various species, and in other rodents. McCulloch (1944, 1946) reports *Schongastia blestowei* and *Trombicula wichmanni* as probable vectors on epidemiological evidence.

THE TARSONEMOIDEA

This superfamily includes a large number of mites that are primarily plant-inhabiting or that infest foods of various kinds. A few species are known to be parasitic, and one species, under certain conditions, may attack man. *Acarapis woodi* Rennie lives in the tracheae of honeybees and produces a serious disease of the adults known as "Isle of Wight disease." Two species have been recorded as invading the tracheae of grasshoppers (Wehrle and Welch, 1925).

Pediculoides ventricosus Newport, the grain itch mite, is a predaceous mite (Fig. 31) that feeds on the larvae of various insects infesting seeds, grains, plants, or their products. It feeds on the larvae of the Angoumois grain moth (*Sitrotroga cerealella* Oliv.), the pink bollworm of cotton (*Pectinophora gossypiella* Saunders), the joint worms (*Isosoma grande* Riley and *I. tritici* Fitch), the bean and pea weevils (*Mylabris quadrimaculatus* Fabr. and *M. obtectus* Say), and others. There is marked sexual dimorphism in this mite (Fig. 31). The abdomen of the fertilized female becomes greatly swollen as the eggs hatch within the body of the mother, and the young are retained till they reach sexual maturity. A single female may give birth to as many as 270 sexually mature mites. In seeds, grain, straw, cotton, beans, or other plant material infested with the insect larvae noted above, this mite may occur in enormous numbers. Man is attacked when handling such infested material or sleeping on infested straw, or when he in other ways comes in contact with large numbers of the mites. On man their bites produce a rashlike dermatitis, which may cover the entire body (Fig. 37). The rash appears 12 to 16 hours after the attack and consists of wheals and papules of varying size. Vesicles or pustules may develop, and the attacked areas may become very red and have

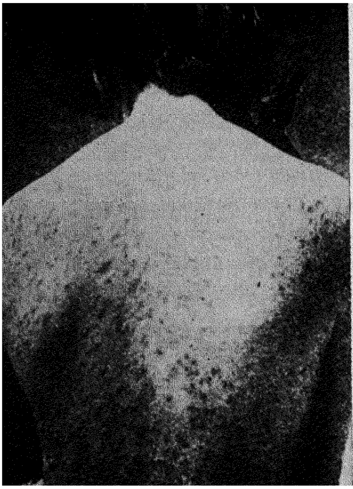

Fig. 37. Lesions produced on man by the bites of *Pediculoides ventricosus.* (After Webster.)

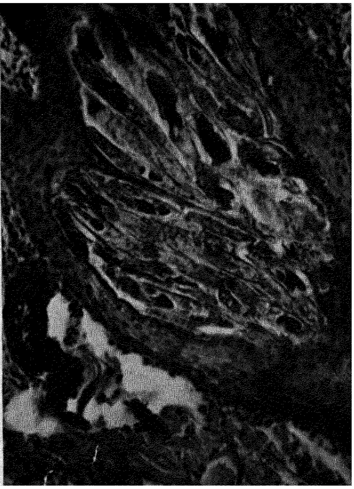

Fig. 38. Demodex canis. Base of a sebaceous gland of a dog packed with *Demodex canis.*

a burning, itching sensation. Fever and sweating are recorded as concomitants in some cases. Ciarrocchi (1928) describes an epidemic of pruriginous dermatitis in Italy caused by this mite. Its attacks have been recorded from widely scattered regions of the world. Diagnosis of this rash must be based on the occupation or sleeping habits of the patient and the discovery of the mites. Treatment consists of avoiding further infestation; recovery will be rapid. In severe cases the rash may be reduced by bathing in warm, soapy water, followed by the application of a mild talcum powder.

THE TYROGLYPHOIDEA

The mites belonging to this superfamily are minute and abound on dried fruits, other foodstuffs, roots, and bulbs. Man becomes infested from handling infested products. Vanilla pods and beans are often heavily infested, and a dermatitis, known as "vanillism," frequently occurs among vanilla workers. It is believed to be caused by the mite *Tyroglyphus siro* Linn. Copra itch is a common dermatitis among workers in the copra mills and was first described by Castellani in Ceylon. It is caused by *Tyroglyphus longior* var. *castellani* Hirst. This dermatitis may affect copra workers in all parts of the world. A so-called "grocers' itch" is caused by *Glyciphagus prunorum* Hermann (*G. domesticus* de Geer), which often abounds in grocery stores. The dermatitis caused by these mites may be mistaken for scabies or other types of skin diseases. For the purpose of diagnosis the history of the patient's work may often give a clue to the causative agent. Treatment consists of various ointments and the avoidance of mite-infested plants or foodstuffs.

As mites of this family abound in foodstuffs, they have been recorded many times from fecal examinations. Whether they cause any trouble in the intestinal tract does not seem to be known. Mekie (1926) has reported the infection of the urinary tract by three species, *Tarsonemus floricolus* C. and F., *Glyciphagus domesticus* de Geer, and *Tyroglyphus longior* Gerv. He also reviewed previously reported cases. Hinman *et al.* (1934) reported a case of intestinal myiasis due to *Tyroglyphus longior* Gerv. It is difficult to conjecture how such infection takes place except through uncleanly habits.

THE DEMODICOIDEA

The Demodicoidea, the hair-follicle mites, are a highly aberrant group of mites. They are parasitic in the hair follicles and sebaceous glands of mammals. They are very elongate (Fig. 32), the legs are reduced to mere stumps, the abdomen is vermiform, and the mouth parts are modified, minute, and fitted for piercing. The superfamily contains but a single family, the Demodicidae, and one genus, *Demodex*. The hair-follicle mites of different animals are extremely difficult, if not impossible, to differentiate as distinct species. Hirst (1919) has brought more or less order out of the chaos and has redefined the various forms.

Demodex folliculorum Simon is the hair-follicle mite of man. It is abundant in some countries, but it is said to be rare in North America. It lives deep down in the hair follicles and sebaceous glands. The entire life cycle is passed on the host so that the infection gradually spreads. It is not considered of any pathogenic importance to man.

Demodex canis Leydig (Figs. 38,39) attacks dogs and is cosmopolitan in distribution. It causes the follicular or red mange of the dog. The disease is serious and there is no known successful treatment. *D. cati* Mégnin parasitizes the cat; *D. bovis* Stiles, cattle; *D. equi* Raillet, horses. Other species are found on different mammals. Baker (1946) reports a serious infection of a cow with demodectic mange. The mange appeared as enlarged nodules, and each nodule when opened contained an enormous mass of the mites in all stages. This type of mange is apparently very rare. Several workers have recorded *D. canis* parasitizing man, but Hirst regards these cases as doubtful.

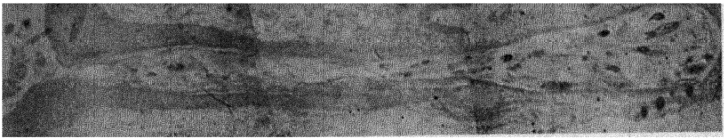

Fig. 39. A gland from a dog, showing *Demodex canis* along the entire gland.

THE CLASS PENTASTOMIDA

The tongue worms and their allies

This aberrant group has had a varied taxonomic career, having been placed, at one time or another, with the Cestoda, Nematoda, and Hirudinea. Van Beneden (1848) placed it in the Arthropoda, and Sambon (1922) established its position as in the Acarina though now it is regarded as a distinct class.

The adults are elongate, legless, cylindrical, or flattened worms divided externally by conspicuous rings that are not true segments. The mouth is provided with a chitinous armature, which is located before, behind, or between two pairs of hollow, retractile, fanglike hooks (Figs. 40,41). The sexes are distinct, the males smaller than the females. There is no separation of the head, thorax, or abdomen. Anteriorly the most conspicuous features are the hollow fangs or retractile hooks. At their bases open a number of glands, the secretion of which is supposed to have a hemolytic action. The internal structure is very simple. The mouth opens into a pharynx, which connects with a short esophagus. The pharynx is supplied with muscles, which undoubtedly serve to exert a sucking action. The esophagus opens into the mid-gut or stomach, which is somewhat capacious and extends the entire length of the body to the rectum. There is no trace of circulatory or respiratory organs. The nervous system is vestigial. The main organs appear to be for reproductive purposes as the ovaries and testes are well developed. In the females the opening of the vagina is either at the anterior or posterior end of the body.

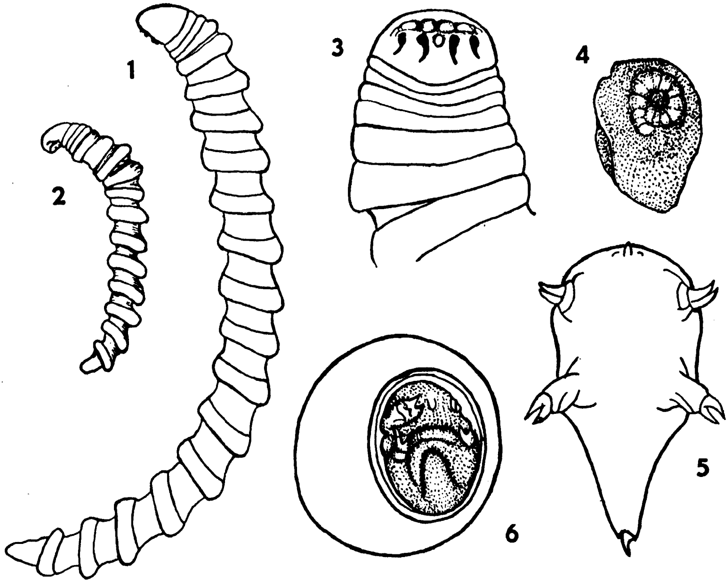

Fig. 40. (*1*) *Armillifer armillatus,* female. (*2*) Male. (Both drawn to the same scale.) (*3*) Head of *A. armillatus* to show the fangs. (*4*) Nymphal stage of same species in liver. (*5*) Recently hatched larva of same species. (*6*) Fully developed embryo within the egg of *Porocephalus subulifer.* (All modified from Sambon.)

Heymans and Vitzthum (1936) in an extensive paper divide the Pentastomida into two orders, which may be separated by the following scheme:

1. Hooks located on fingerlike processes or slight swellings of the body back of the mouth; genital opening anterior in both sexes .... Order *Cephalobaenida*
   Two families: *Cephalobaenidae* (in lungs of snakes and lizards); *Reighardiidae* (in air sacs of birds) 2
2. Hooks not so located but arranged on each side of the mouth either in a straight, curved, or arched line; genital opening of the female posterior .... Order *Porocephalida*
   Two families: *Porocephalidae* (body cylindrical; adults in lungs of reptiles; young in a great variety of vertebrates including man); *Linguatulidae* (body flattened; adults in nasal passages of dog and cat family; young in all sorts of mammals including man)

As far as known all species of this class have a complicated life cycle, the larval and nymphal stages in one host and the adults in another. *Linguatula serrata* occurs in the adult stage in the nasal passages and frontal sinuses of dogs (occasionally in man and some herbivores), where they suck blood. They cause a severe catarrh, suppuration, and bleeding. The eggs of the parasite are discharged in the mucus and wastes from the nostrils, infecting water or vegetation. If these eggs are eaten by rabbits, sheep, goats, etc., or by man, the larvae escape from the eggs, migrate through the intestinal walls, and usually locate in the liver or other organs where the nymphal development takes place. In a short time the larva (Fig. 40) becomes encapsulated by the host-tissue reaction and nymphal development proceeds. In about five or six months the nymphs become mature; they then possess two pairs of hooks and measure 4 to 6 mm. in length. The body is divided into numerous rings, each bordered posteriorly by a row of closely set spines. Within the cysts the nymphs may live at least two or three years. If, however, raw liver or other organs containing these nymphs are eaten by dogs or man, the nymphs gain access to the nasal passages via the mouth or esophagus and there reach maturity. In Europe dogs are frequently parasitized and humans not uncommonly harbor the nymphs in their internal organs. Hobmaier and Hobmaier (1940) give a clear account of the life cycle of *Linguatula rhinaria,* a parasite of brown rats and dogs. Their account differs in many details from the records of other workers.

In Africa man is frequently parasitized by *Armillifer armillatus* (Fig. 40). This species is found as a mature parasite in pythons and other snakes; its intermediate hosts are primarily monkeys and apes, although carnivores and other animals have also been reported as infected. The natives of certain parts of

Africa regard python steaks as delicacies, and as a result frequently become infected by eating raw meat. Infection may also take place by eating raw vegetables or drinking water contaminated with the eggs of the parasite. Human infection is common in many parts of West Africa, the nymphs being recovered at autopsies. Cannon (1942) reports the death of an African woman due to an extremely heavy infection of the colon by encysted nymphs of this species. *A. moniliformis* is parasitic in the respiratory tract of pythons, and records of human infections are rather rare (three so far recorded, one from Manila, one from Sumatra, and one from a Tibetan in China).

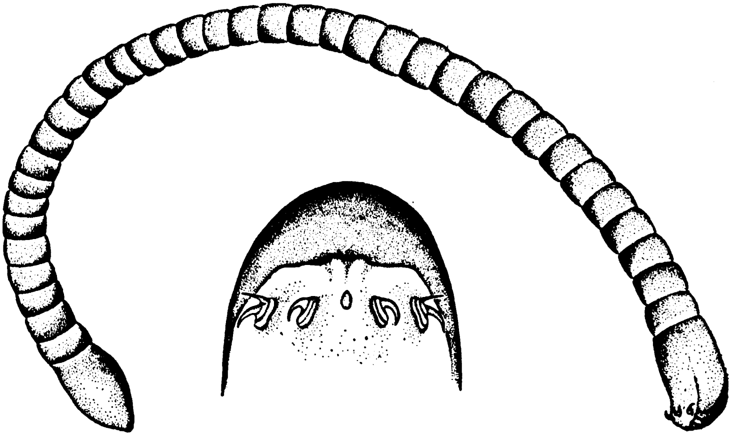

Fig. 41. Porocephalus clavatus. Mature female from the lung cavity of a South American snake. The central figure shows the head with the four characteristic fangs.

Porocephaliasis is the usual term employed to designate human infection with species of Pentastomida. Sambon in 1910 and 1915 summarized the known human cases up to that time. It appears that when few nymphs are present in man the ill effects are not serious; when large numbers occur the effects may be dangerous, but there is no method of diagnosing their presence. Most of the present information of human infections is based on findings at autopsies or from abdominal operations.

In America two cases of porocephaliasis are on record. As no species of *Armillifer* are known from the Americas, it is thought the infections may have been due to the nymphal stage of *Porocephalus crotali* of rattlesnakes or an allied form. Penn (1942) reports *P. crotali* as being found commonly in the larval and nymphal stages in muskrats (*Ondatra zibethica rivalica*) in

Louisiana and the adults in the water moccasin (*Agkistrodon piscivorus*). The adults live in the lung cavities of the snakes and the eggs are discharged in the sputum. When the infected sputum is eaten by the muskrat, the eggs hatch in the small intestine and the larvae migrate to the liver and lungs, where they become encapsulated in the tissues. The nymphs become mature in about three months. When infective muskrats are eaten by the water moccasin the nymphs migrate up the esophagus and into the tracheae and lungs, where they develop to adults.

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CHAPTER V

The Hexapoda: Insects

THE class Hexapoda contains an enormous assemblage of species, everywhere present and always abundant in all regions of the world. They are small animals possessing a body made up of transverse segments; their segments are grouped into three distinct regions, the head, thorax, and abdomen. The segmentation shows most distinctly in the abdomen and thorax, whereas in the head the segments have become fused, forming a highly chitinized box. The number of segments is generally stated as twenty. These are distributed as follows: 6 constitute the head, 3 compose the thorax, and 11 form the abdomen. Typically each segment of the primitive arthropod bore a pair of appendages, but in insects many of these have been lost. There are readily visible but three pairs, the legs, which are attached to the segments of the thorax. The other appendages have been lost (as in the abdomen) or modified for other purposes (as the mouth parts, antennae, eyes, and external genital appendages). In addition, the great majority of insects possess a pair or two pairs of wings attached to the dorsolateral angles of the second and third thoracic segments. Insects breathe by means of a highly complicated system of tracheae, which penetrate every portion of the body and open externally by special orifices, the spiracles, situated at the sides of the body.

The animals, as characterized above, constitute a vast assemblage, numbering nearly a million described species. They far outnumber, in species, all other animals combined, while in individuals their vast multitudes are like the sands of the sea—uncountable. Who can estimate the ants of a single hillside, the aphids of an orchard, or the flies of a city? As a group, insects are considered to be the most successful of all forms of terrestrial animal life, yet man treats them with scant respect.

EXTERNAL ANATOMY

Externally the body of an insect is composed of transverse segments (20), which may or may not bear appendages. These segments are grouped into three regions, head, thorax, and abdomen (Fig. 42). The surface layer of the body is called the body wall or integument. It is more or less rigid and forms the skeleton within which all the organs and fleshy parts are enclosed; but the external covering is flexible along certain transverse and longitudinal lines and at other points, thus permitting a great variety of movements. The hardened portion of the body wall is due to the deposition of various substances in the chitin and it is variously distributed; usually lines (sutures) delimit the sclerotized areas, which are called sclerites. The arrangement of sclerites and their separating sutures constitutes the major feature of the external anatomy of insects.

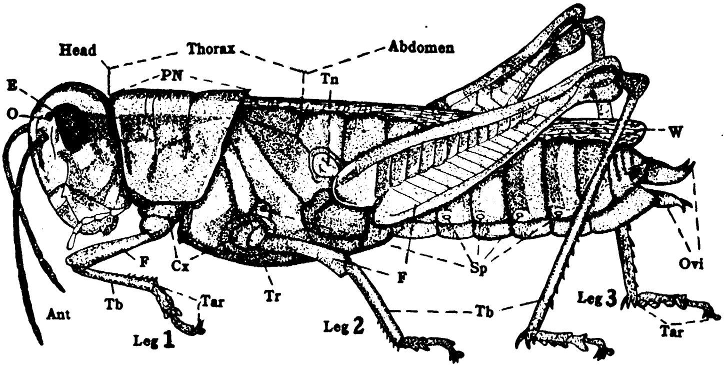

Fig. 42. Lateral view of a grasshopper to illustrate the principal external structures of an insect. (Wings of one side removed.) Ant, antenna; Cx, coxa; E, compound eye; F, femur; O, ocellus; Ovi, ovipositor; PN, pronotum; Sp, spiracles; Tar, tarsus; Tb, tibia; Tn, tympanum of ear; Tr, trochanter; W, wing.

THE BODY WALL

The body wall is a continuous structure, and the apparent segmentation is due to infoldings. It completely surrounds the insect. It also extends internally and forms the lining of the fore and hind intestine; the tracheae are only invaginations of the body wall. The only external openings are the mouth, the anus, the spiracles, and those of the genital organs. The body wall is composed of a single layer of epidermal cells supported on a noncellular membrane (basement membrane). Outside these cells lies the cuticula, a product of the epidermal cells (Fig. 43). The cuticula may be soft and pliable, but it is usually sclerotized into definite areas, the sclerites. The cuticula is not a homogeneous structure. It is stratified into two primary layers, the endocuticula and the exocuticula, and externally it is protected by a very thin layer called the epicuticula (Fig. 43). The two primary layers are composed mainly of chitin, whereas the epicuticula is nonchitinous. Chitin is a soft, pliable substance that is insoluble in water, alcohol, ether, dilute acids, or alkalies. It becomes hardened by the deposition of various substances, mainly in the exocuticula. The epicuticula is very thin and is largely impermeable to water. Most of the pigments are found in the exocuticula. The body wall is rarely smooth externally. On it are small spicules, hairs, spines, ridges, scales, setae, or other excrescences. Many of these are merely projections of the cuticula; others, such as stout spines, glandular hairs, and sense hairs, take their origin from the underlying epidermis.

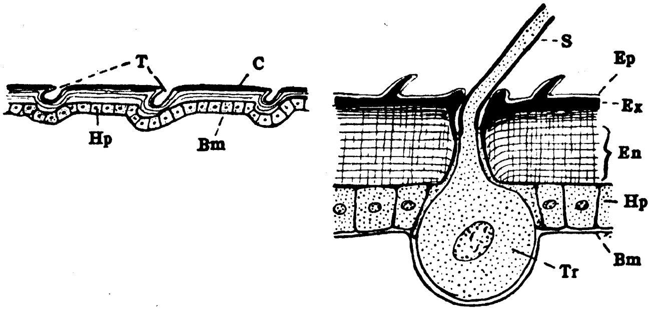

Fig. 43. Left: Diagrammatic longitudinal section of the body wall of an insect. *Right:* More enlarged and detailed sketch of a portion of a body wall to show structure. Bm, basement membrane; C, sclerotized portion of wall of segment; En, endocuticula; Ep, epicuticula; Ex, exocuticula; Hp, Hypodermis or epithelial cells; S, seta; T, the nonsclerotized part of body wall between two segments; Tr, a trichogen cell.

Each segment of the body is composed of a dorsal, lateral, and ventral area. In each of these areas definite parts, sclerites, may occur, and these are separated by sutures. These sclerites bear names, and the terminology becomes quite complex in some of the highly specialized insects. In general, there are recognized for each segment a dorsal sclerite, the tergum or notum; two lateral sclerites, the pleurites; and a ventral sclerite, the sternum. Each of these may be divided into a number of smaller sclerites.

THE HEAD

The head is composed of a number of fused segments (usually regarded as six), and these are so intimately consolidated as to form a hard case, the head capsule. Externally several distinct head sclerites may be recognized, especially in the more generalized insects. Some of these are delimited by sutures, but most of them are fused so that the names refer to areas rather than distinct sclerites. Fig. 42 will illustrate the structure as found in a generalized insect and the terms employed. The main sclerites are the two that form the vertex (Fig. 44); the front or frons, an unpaired sclerite lying in front of the arms of the epicranial suture; the clypeus, a simple sclerite attached to the anterior margin of the front and usually fused with it; the labrum, a flaplike structure attached to the clypeus (this structure is usually included with the mouth parts though it is strictly part of the head capsule); and the genae, paired structures located below and somewhat behind the eye. That portion of the head behind the vertex and the dorsal or posterior surface is known as the occiput. In the more specialized insects the sclerites listed above become fused or modified, but in general the areas are designated by the names indicated.

The Appendages of the Head

The six segments that form the head have not lost all their primitive appendages though they have become highly modified and perform different functions. The appendages still present in the adult consist of the following: (1) a pair of compound eyes, modified appendages of the first head segment; (2) a pair of antennae, which arise from segment two; (3) a pair of mandibles, appendages of segment four; (4) a pair of maxillae, appendages of segment five; (5) a pair of appendages that unite to form the labium, the second maxillae of authors, appendages of segment six. The appendages of segment three are lost in the adult insect though vestiges of them are present in the embryo. The modified head appendages thus consist of eyes, antennae, and mouth parts.

THE MOUTH PARTS: The mouth parts of insects may be quite simple, as in the grasshopper (Fig. 45), or they may be very complicated, as in the bloodsucking insects (Fig. 79) and the muscoid flies (Fig. 47). In general, three types of mouth parts may be recognized, the mandibulate type, the piercing and sucking type, and the nonpiercing and sucking type. There are, of course, many modifications of these types.

The Mandibulate Type (Fig. 45): In this type the mouth parts consist of a labrum, a movable flap attached to the clypeus and overlying the upper margin of the mouth; a pair of mandibles lying directly below the labrum and moving laterally; a pair of maxillae arising below the mandibles and of rather com-

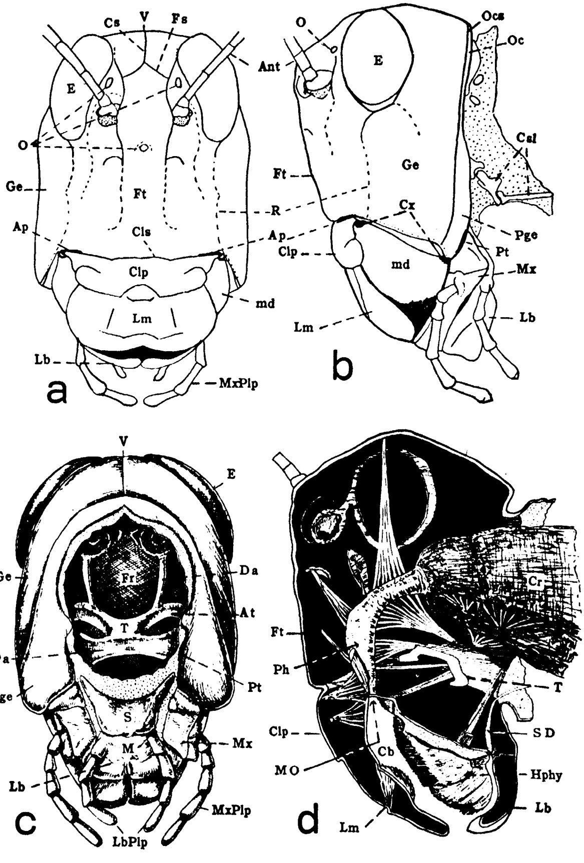
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Fig. 44. (*a*) Frontal view of the head of a grasshopper (*Melanoplus* sp.). (*b*) Lateral view of the head of a grasshopper. (*c*) Posterior view of the head of a grasshopper (*Romalea* sp.). (*d*) Sectional view of head of grasshopper to show the internal structures (*d* modified from Snodgrass). Ant, antenna; Ap, point of invagination for the anterior arm of the tentorium; At, anterior arm of tentorium; Cb, cibarium; Clp, clypeus; Cls, clypeal or epistomal suture; Cr, crop; Cs, coronal suture; Csl, cervical sclerites; Cx, condyles of the mandible; Da, dorsal arm of tentorium; E, eye; Fr, foramen magnum; Fs, frontal suture; Ft, front or frons; Ge, gena; Hphy, hypopharynx; Lb, labium; LbPlp, labial palpi; Lm, labrum; M, mentum of labium; md, mandible; MO, mouth opening; Mx, maxilla; MxPlp, maxillary palpi; O, ocelli; Oc, occipital sclerite; Ocs, occipital suture; Pa, posterior arm of tentorium; Pge, postgena; Ph, pharynx; Pt, point of invagination of posterior arm of tentorium; R, genal suture or ridge; S, submentum of labium; SD, salivary duct; T, tentorium with its arms; V, vertex.

plicated structure; and a labium, closing the lower surface of the mouth and formed by the fusion of a pair of appendages (the second maxillae). On the under surface of the labrum and forming the roof of the mouth is a fleshy organ known as the epipharynx (Fig. 45). It is supplied with sense hairs and is supposed to function as an organ of taste. This structure becomes highly developed in many sucking insects and serves as part of the piercing apparatus as well as part of the channel through which blood is drawn. (Examples: mosquito, Fig. 97; tabanus, Fig. 156.) From the floor of the mouth cavity, at the base of the labium, there arises a fleshy organ, the hypopharynx or lingua. The hypopharynx bears the opening of the common salivary duct and in many insects becomes an important part of the mouth.

The mandibulate type of mouth parts is regarded as the primitive arrangement of the head appendages entering into the formation of the organs for obtaining food. These appendages have become highly modified in many insects and, in some cases, as in the lice and muscoid flies, are so changed that the parts have not been definitely homologized with those of the primitive type. The various types of mouth parts found in bloodsucking insects are discussed more in detail under the different groups but one or two simple bloodsucking types may be compared with the mouth parts of the grasshopper.

Mouth Parts of the Bedbug (*Cimex lectularius*): In the bedbug the mouth parts are rather highly specialized. The labium (Fig. 46 La) has become greatly elongated and divided into three well-defined segments. Along its dorsal surface there is a groove or gutter within which lie the piercing organs, the mandibles and maxillae. The segments of the labium are flexible and can be telescoped on each other by internal muscles. Each mandible is a delicate, chitinous, needlelike rod, which arises deep in the head and terminates in a sharp point, the distal part being supplied with fine recurved teeth (Fig. 46 M). The maxillae (Mx), arise close beside the mandibles but are stouter and slightly longer. They are grooved on the inner face and, just in front of the hypopharynx, form, by apposition, two canals (Fig. 46). They are interlocked throughout their entire length and firmly adhere even when dissected out of the head. In cross section the two canals are distinctly shown, the larger one serving as the food channel up which the blood is drawn by the pharyngeal pump; the smaller one is the channel down which the secretions of the salivary glands are forced into the wound by the salivary pump. The labrum or labrum-epipharynx is a large structure lying over the base of the labium. On the under surface, lying at the base of the labium, is the fine-pointed hypopharynx (Fig. 46 Hyp) through which is discharged the salivary secretion into the groove formed by the maxillae. The salivary pump is a complicated

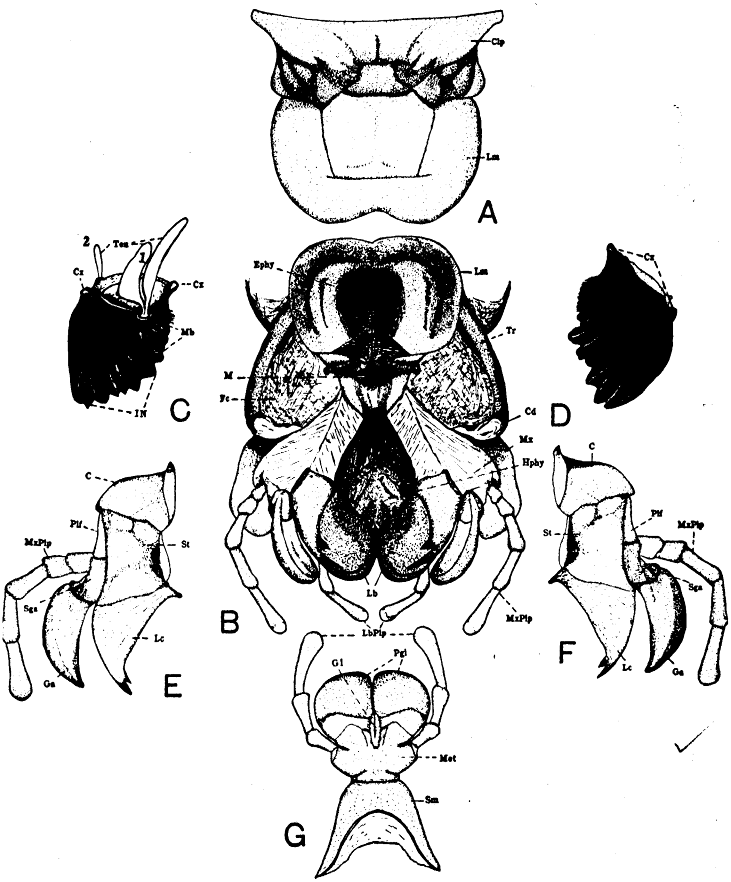
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Fig. 45. Mouth parts of a grasshopper. (*A*) Frontal view of the labrum attached to the clypeus. (*B*) Looking into the mouth of a grasshopper with the mandibles removed and the labrum turned back. (*C*) The lower side of a mandible with the tendons in place. (*D*) The upper side of a mandible. (*E*) and (*F*) The right and left maxillae as viewed from the lower or ventral side. (*G*) The labium as viewed from the lower side. C, cardo; Cd, socket for condyle of mandible; Clp, clypeus; Cx, condyles of mandibles; Ephy, epipharynx; Fc, area over which fits the base of the mandible; Ga, galea; Gl, glossa; Hphy, hyopharynx; IN, cutting teeth of mandible; Lb, labium; LbPlp, labial palpi; Lc, lacinia; Lm, labrum; M, opening into mouth; Mb, molar portion of mandible; Met, mentum; Mx, upper or dorsal surface of maxilla; MxPlp, maxillary palpi; Pgl, paraglossae; Plf, palpiger; Sga, subgalea; Sm, submentum; St, stipes, Ten, tendons; Tr, torma.

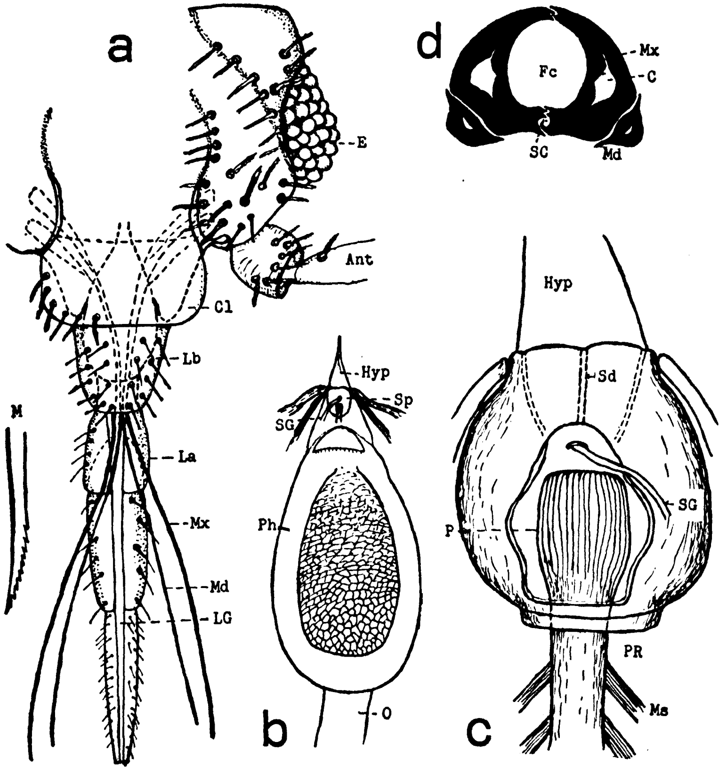

Fig. 46. The mouth parts of the bedbug (*Cimex lectularius*). (*a*) Frontal view of the mouth parts and part of the head. (*b*) Ventral view of the pharynx and salivary gland connections with the hypopharynx. (*c*) The salivary pump partially opened. (*d*) Cross section of the maxillae and mandibles. Ant, antenna; C, extension of body cavity into maxilla; Cl, clypeus; E, eye; Fc, food channel; Hyp, hypopharynx; La, labium; Lb, labrum; LG, labial gutter; M, tip of mandible, greatly enlarged; Md, mandible; Ms, muscles that move the piston; Mx, maxilla; P, piston head; Ph, pharynx; PR, piston rod; O, esophagus; SC, salivary channel; Sd, salivary duct; SG, common duct of salivary glands; Sp, salivary pump.

organ, but its structure and function have been elucidated by Patton and Cragg (1913) and Puri (1924). It is located on the ventral surface of the hypopharynx; it is cup-shaped in general appearance and about one-tenth the size of the pharyngeal pump. Its posterior end is closed by an elastic membrane, a part of which is invaginated to form a chitinized piston (Fig. 46). Posteriorly the piston is continued as a flattened rod to which retractor muscles are attached on each side. The salivary duct opens into the pump on the ventral side by a crescent-shaped opening. The working of the pump is brought about by the movement of the piston. When the piston is withdrawn, salivary secretion is drawn into this chamber. The relaxation of the retractor muscles is followed by the recoil of the elastic posterior membrane of the pump, which forces the piston into the chamber and the saliva is sent down the duct in the maxillae into the wound. The recoil of the piston closes, at the same time, the opening of the salivary duct leading from the glands. The saliva in bloodsucking insects seems to perform certain definite functions, either to prevent coagulation or to induce blood flow to the invading mouth parts.

Another important organ in connection with the bloodsucking type of mouth parts is the pumping pharynx or pharyngeal pump, an organ whose special function is to pump the blood from the host and pass it on to the intestine. In the bedbug the organ is well developed. It is pear-shaped in outline, but flattened dorsoventrally. In sectional view the lumen appears as a transverse slit. The pumping action is brought about by powerful dilator muscles attached to the dorsal surface; these dilate the pharyngeal cavity, and blood flows in through the food channel (Fig. 46). The relaxation of the muscles allows the resilient chitinous walls to come together and thus probably forces the blood on through the esophagus.

Mouth Parts of Other Bloodsucking Insects: In other bloodsucking insects various modifications occur. In the mosquito (Fig. 97), it is the labrum-epipharynx that forms the food channel. These organs, together with the mandibles and maxillae, constitute the piercing apparatus. The salivary secretion is pumped into the wound through a channel in the hypopharynx. The pharyngeal pump is well developed and functions as in the bedbug, though here the pharynx must connect with a different food channel. The structures employed by various insects in piercing a host and withdrawing blood are in need of more detailed study, and some of these problems will be stressed under the discussion of the various bloodsucking groups.

Mouth Parts of Some Muscoidean Flies: Another type of mouth parts of great interest to the medical entomologist is that found in many of the muscoidean flies as, for example, the housefly, the flesh flies, the bluebottle flies, and others. Here the food is taken in one of three ways: (1) the flies may obtain their food in liquid form as nectar, milk, sugar solutions, the liquid exudates of decaying substances (as pus, fecal matter, sewage, etc.), perspiration, serum exudates from wounds, moisture from around the eyes, or other sources; (2) or they may liquefy soluble substances such as sugar by regurgitating liquid from their intestines or by using the salivary secretion and then suck up such fluids by their mouth parts; (3) or they can ingest larger particles by applying the mouth opening directly to soft substances. This type is very complicated and may be best illustrated by the mouth parts of the housefly.

In the housefly the mouth parts constitute an elongated proboscis, which, when not in use, is partly withdrawn into the head capsule. When the fly is about to feed, the proboscis is extended by compression of the body, thereby forcing blood into the open spaces of the proboscis, and the tracheae and air sacs become distended with air (Fig. 47). The proboscis then hangs downward from the head capsule. This distension may be produced artificially by soaking the head in 10 per cent caustic potash, then placing it under a dissecting microscope, and pressing on it with a needle; the proboscis and labella may be extended and partially contracted at will. The proboscis may be divided into three distinct regions—the rostrum, the haustellum, and the oral disc (Fig. 47).

THE ROSTRUM (Fig. 47 R): In side view the rostrum appears like a truncated pyramid, the base attached to the head capsule. Its wall (W) consists of a rather tough chitinous membrane that is attached to the ventral margin of the head and is continuous with that of the haustellum and the oral disc. Within the membrane is the large pharyngeal sclerite or fulcrum (Fig. 47 Fu), and within the fulcrum lies the pumping pharynx and its dilator muscles. In side view the fulcrum appears like a Spanish stirrup iron, while the frontal aspect presents an inverted vaselike appearance. The sides of the fulcrum are roughly triangular in outline and are produced at their proximal ends into a pair of stout cornua. The anterior angles are joined by the clypeus (*tormae* of Peterson) and the anterior arch (Fig. 47). Posteriorly they are joined by a thinner convex plate, the posterior plate, which forms the rear wall of the pharynx. The anterior wall of the pharynx consists of a thin chitinous plate, thickened along its median line to form a sharply delimited chitinous rod, the median ridge. To this ridge are attached the dilator muscles of the pharynx. Its distal end terminates opposite, and in close contact with the prepharynx (hyoid sclerite). The pharynx unites at its proximal end with the esophagus, and its distal end joins the tube formed by the mouth parts by way of the hyoid sclerite, which surrounds the buccal opening. By means of the retractor muscles the anterior wall of the pharynx is withdrawn from the posterior wall, and by this action liquid food is sucked up through the mouth parts and passed into the esophagus. Below the fulcrum, on either side of the middle line, there are two slightly chitinized plates. From each of these arises a single-jointed, somewhat club-shaped maxillary palpus) Near the border of the maxillary plates there arises on each side of the fulcrum a sinuous, strongly sclerotized rod; the apices of these rods articulate in small pits at the sides of the broad base of the labrum-epipharynx and function in the extension and retraction of the proboscis (Below the palpi the rostrum narrows and merges with the haustellum.)

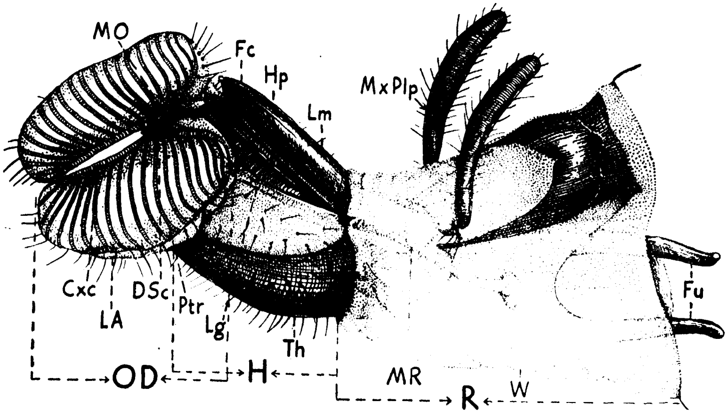

Fig. 47. A somewhat lateral view of the proboscis of the housefly (*Musca domestica*). R, rostrum; H, haustellum, OD, oral disc; MO, mouth opening; Cxc, a main collecting channel of the pseudotracheae; DSc, discal sclerite; Fc, food channel between the hypopharynx (Hp) and the labrum (Lm); Fu, fulcrum seen in outline beneath the chitinous membrane (W); Hp, hypopharynx; LA, labella; Lg, labial gutter; Lm, labrum; MR, maxillary rods (stipes); MxPlp, maxillary palpi; Ptr, pseudotracheae; Th, theca; W, membrane of proboscis.

THE HAUSTELLUM (Figs. 47,48): The haustellum (H) is attached to the distal end of the rostrum and gradually narrows to its junction with the oral disc. In the housefly, as in many of the higher Diptera, all the mouth parts are not present. The mandibles and maxillae are lacking though the palpi of the maxillae still persist. The mouth parts consist of the labrum-epipharynx, the hypopharynx, and the labium. The rear portion of the haustellum is the labium. Its structure is complicated and not well understood. The posterior surface consists of a large, concave sclerite, the mentum or theca, which is articulated with the base of the haustellum; its apex rests on peculiar rods that articulate with the oral disc. The anterior face of the labium is deeply grooved (labial groove), and the margins of the groove are supported by stout rods (Fig. 48 LR) that extend from the base to articulate with the discal sclerite. The mentum and the anterior groove are connected on each side by tough membranes. Lying in the labial groove or gutter are the labrum-epipharynx and the hypopharynx. The labrum-epipharynx (Lm) is in front. It consists of an elongate, pointed organ that is deeply channeled on its posterior face (Fig. 48). The hypopharynx lies directly behind the labrum-epipharynx; it is an elongate bladelike structure (Hp) with a groove in its anterior face. The margins of these two fit closely into each other and thus form the food channel (Fc). The tips of the labrum-epipharynx and hypopharynx extend to the opening formed by the discal sclerite; their bases are united and lead to the mouth opening, which lies between them.

THE ORAL DISC (Figs. 47,48): The oral disc (OD) consists of the discal sclerite (DSc) and the labella, the two large lobes that arise from the discal sclerite. The labella are shown fully expanded in the figures. When not in use they are greatly reduced in size. The oral disc articulates to the distal part of the haustellum by means of two joints. The anterior joint is formed by the junction of the labellar rods to the discal sclerite by means of tendons. The discal sclerite is somewhat horseshoe-shaped, the opening being anterior; posteriorly there extends a stout thickening of the sclerite. This sclerite surrounds the mouth or oral opening, and to it are attached the pseudotracheal membrane and the prestomal teeth. The posterior joint of the oral disc is formed by a pair of rods (the sigma or metofurcal bars) that rest on two arms of the triradiate labellar sclerite or furca. These rods arise from the forks of the mentum (Fig. 48 Th).

The two labellar lobes are completely separated from each other by a deep fissure, which is continuous anteriorly with the labial groove or gutter; the fissure extends some distance on the posterior face. Each labellum contains a large hemocele and is filled with blood when extended. In the resting condition the two inner walls of the labella are in close contact, but when feeding they are widely separated. As the walls are very soft they can be molded to any surface on which the fly is feeding. The inner surface of each labellum is traversed by a series of channels that resemble tracheae, hence are called "pseudotracheae" (Figs. 47,48 Ptr). Through these pseudotracheae the fly sucks up its liquid food. As the size of the opening to these channels determines what materials the fly can ingest, the structure of these organs is of the utmost importance. The inner wall of each labellum consists of a very thin, structureless membrane in which lie the pseudotracheal channels. These channels all converge to the prostomum or opening bounded by the discal sclerite. In each labellum are 30 to 32 of these grooves; the upper 9 or 10 and the lower

15 or 16 unite to form collecting channels (Figs. 47,48 Cxc), and the middle 5 or 6 open directly into the prostomum. Each pseudotracheal channel is kept open by means of incomplete rings of chitin. Each chitinous ring is bifid at one end and simply expanded at the other. The rings are closely set and alternate so that a bifid end faces an expanded end, and then an expanded end faces a bifid end. Looking along the surface of a channel there appears a series of alternate bifid and expanded ends of chitinous rings (Fig. 48 *d,e,f*). The membrane of the labellum is stretched taut over all these rings except between the bifid ends and the line between the expanded ends and the forks. Therefore, the only openings into the channel itself are between the forks of the bifid end of each ring and a zigzag fissure extending the whole length of the channel. The openings between the bifid ends have been called the "interbifid grooves." During feeding the membrane is stretched so taut that the zigzag fissure is practically closed and the only food that can enter is through the interbifid grooves. The size [1] of the interbifid grooves determines the size of the solid particles that can pass into the food channel. This position of feeding has been termed by Graham-Smith "the filtering position."

By separating the labella further there is brought into play the prestomal teeth (Fig. 49). These teeth arise from the lateral margin of the discal sclerite, five on each side. Each tooth consists of a chitinous strip, serrate on its distal extremity, and lies between the openings of two pseudotracheae. Graham-Smith (1930) has shown that instead of one row of prestomal teeth there are four rows in the blowfly (*Calliphora erythrocephala*). This also appears to be the condition in the housefly. The first three chitinous strips that surround the pseudotracheal openings into the oral cavity are not bifid but sharply pointed (Fig. 49 O). These may correspond to the extra teeth described for the blowfly. Following these are the ordinary chitinous rings that keep the pseudotracheae open.

Recently Graham-Smith has described three methods of feeding by the blowfly; the housefly, in all probability, feeds in the same fashion. The first method, the filtering method, has already been described. By further separat-

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[1] Graham-Smith has measured these interbifid spaces and the channels in several of our common flies. These are here appended.

	Pseudotracheae, diameter (mm.)		Interbifid spaces, diameter (mm.)	
	Proximal end	Distal end	Proximal end	Distal end
Calliphora erythrocephala	0.02	0.01	0.006	0.004
Sarcophaga carnaria	0.02	0.01	0.005	0.004
Lucilia caesar	0.02	0.01	0.006	0.004
Fannia canicularis	0.016	0.008	0.006	0.004
Musca domestica	0.016	0.008	0.004	0.003

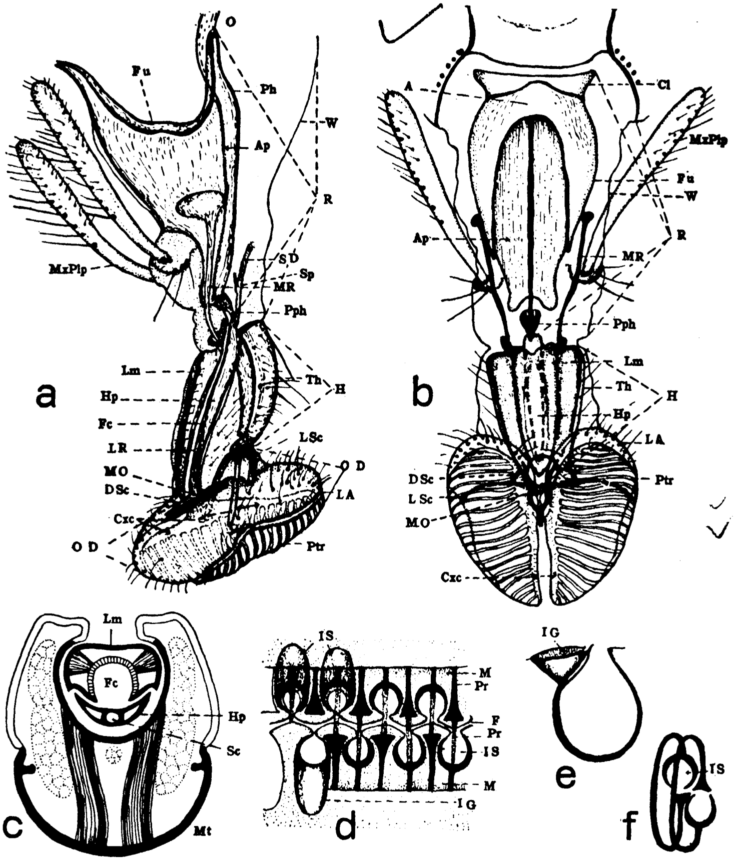
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Fig. 48. Detailed illustrations of the mouth parts of the housefly (*Musca domestica*). (*a*) Lateral view of the proboscis of the housefly. (*b*) Frontal view of the proboscis with the labella expanded. (*c*) Cross section (somewhat diagrammatic) of the middle of the haustellum. (*d*) View of a pseudotracheal channel (highly magnified) as seen through the integument of the labellum; the right half illustrates the details of a channel with the chitinous rings in place; the upper left side shows two interbifid grooves in the integument with the chitinous rings showing through; the lower left corner shows a single interbifid groove which leads to an interbifid space. (*e*) A single chitinous ring in side view showing the attachment of the interbifid groove to the forks of the ring. (*f*) Two chitinous rings as they are arranged in a pseudotracheal channel (partial side view). H, haustellum; OD, oral disc; R, rostrum; A, anterior arch of fulcrum; Ap, anterior wall of pharynx; Cl, clypeus; Cxc, main collecting channels; DSc, discal sclerite; F, fissure along the surface of the pseudotrachea; Fc, food channel; Fu, fulcrum; Hp, hypopharynx; IG, interbifid groove; IS, interbifid space, LA, labellum; Lm, labrum; LR, labellar rods;

ing the labella the prestomal teeth can be brought into action and used for scraping—the scraping position. By an extreme folding back of the labella the mouth or oral opening can be brought into direct contact with the food, and then comparatively large objects can be ingested, as the eggs of helminths. By various manipulations of these methods the fly can feed on a great variety of substances. Furthermore, liquid can be regurgitated (the vomit drop) to dissolve what has been scraped loose (Fig. 50). Graham-Smith also states that the prestomal teeth, moistened with infected vomit, appear to be excellent instruments for the intradermal introduction of pathogenic organisms. Sites on the body most likely to be selected for scraping are mucus and conjunctival surfaces, recent abrasions, and wounds.

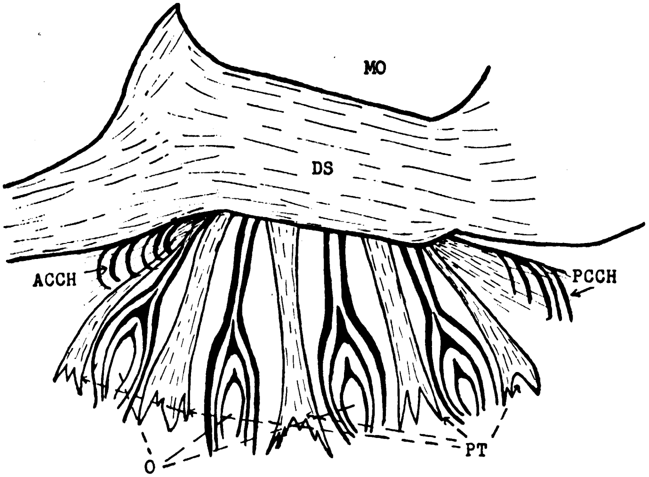

Fig. 49. Looking into the mouth opening of the housefly (only a small part is shown). ACCH, anterior collecting channel; DS, discal sclerite; MO, mouth opening; O, openings to the pseudotracheal channels, PCCH, posterior collecting channel; PT, prestomal teeth.

The mouth parts of other insects that affect man are briefly discussed under the different species described in the following pages.

LSc, labellar sclerite; M, membranous portion of the pseudotracheal channel; MO, opening to the food channel; MR, maxillary rods (stipes); Mt, mentum; MxPlp, maxillary palpus; O, esophagus; Ph, pharynx; Pph, hyoid or prepharyngeal sclerite; Pr, pseudotracheal ring of chitin (the dotted portion indicates the position of the ring at the rear of the channel); Ptr, pseudotracheae; Sc, salivary channel in hypopharynx; SD, salivary duct; Sp, salivary pump or syringe; Th, theca or mentum; W, membranous wall of proboscis.

THE ANTENNAE: The antennae are the modified appendages of the second head segment. Each antenna arises from a small antennal sclerite situated in the antennal fossa. The antennae show various modifications in the different orders and names have been applied to them such as setaceous, filiform, clavate, and capitate. Some of the types found in insects of medical importance are shown in Fig. 51. The number of antennal segments varies widely. The first segment is known as the scape and the second as the pedicel; the remaining segments constitute the flagellum (Fig. 51). The various functions of the antennae are not well known. It has been fully established that the sense organs of touch and smell are present on the antennae and possibly also some of the organs of taste.

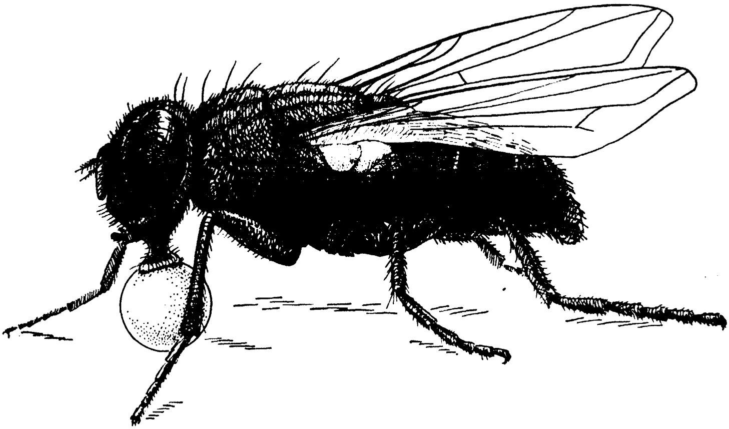

Fig. 50. The housefly, *Musca domestica,* showing the vomit spot at the tip of labella. (Modified from Hewitt.)

THE THORAX

The thorax is the second region of the body. It is attached to the head by an intersegmental region known as the neck. The neck is not sclerotized except for a few small sclerites, the cervical sclerites. The thorax consists of three segments and bears the wings and legs. The segments are known as the prothorax, mesothorax, and metathorax (Fig. 52). The terms pro, meso, and meta are used to designate the first, second, and third segments of the thorax and also the various parts of these segments. For example, the protergum, proepisternum, etc., refer to the tergum and episternum of the prothorax. The pleuron of each thoracic segment is usually divided into two sclerites—the anterior one being called the episternum (Fig. 52 Eps) and the posterior the epimeron (Epm)—and these bear the prefixes, pro, meso, or meta to indicate to which segment they belong. Each segment, in its simplest form, consists of a dorsal region, the tergum or notum; a ventral region, the sternum; and two sides, the pleura (singular pleuron) or pleurites. Each of these regions may consist of one or several sclerites separated by sutures. A rather simple type of thorax is that of the grasshopper (Fig. 52). It is more or less cylindrical in shape. Here the tergum (PN) of the prothorax is greatly enlarged; it overlies a large part of the mesothorax and extends down on the sides to near the

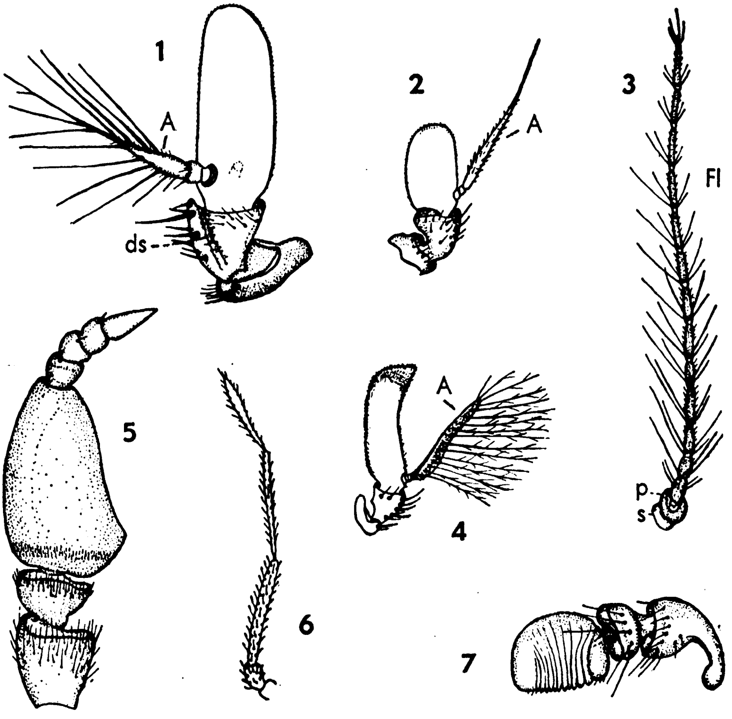

Fig. 51. Various types of insect antennae. (*1*) *Musca domestica.* (*2*) *Wohlfahrtia vigil.* (*3*) *Aedes aegypti.* (*4*) *Glossina palpalis.* (*5*) *Tabanus flavus.* (*6*) *Cimex lectularis.* (*7*) *Xenopsylla cheopis.* (Not drawn to the same scale.) A, arista; ds, dorsal suture or seam; Fl, flagellum; p, pedicel; s, scape.

attachment of the first pair of legs. Only a small portion of the lateral wall is visible—the episternum (Eps$_1$) of the prothorax; the epimeron is entirely concealed and lies underneath the lower end of the tergum.

The mesothorax is shown in dotted lines beneath the pronotum. The episternum (Eps$_2$) and the epimeron (Epm$_2$) are well developed, and from their lower ends arises the second pair of legs. The metathorax is also large and the pleurites (Eps$_3$ and Epm$_3$) are well outlined. Their tergal portions underlie the pronotum and the wing bases. It is well to note that the meso- and metathorax of the grasshopper are each much larger than the prothorax, owing to the presence of wings. This enlargement is to provide for the processes for wing attachment and the large muscles needed to move these

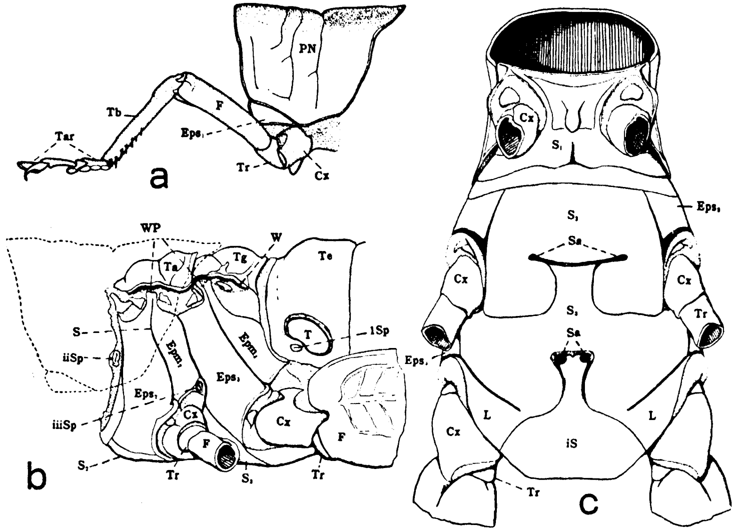

Fig. 52. The external structure of the thorax of a grasshopper (*Melanoplus differentialis*). (*a*) Prothorax with the leg attached. (*b*) Lateral view of the meso- and metathorax (pterothorax) with the first segment of the abdomen; the prothorax sketched in outline. (*c*) Ventral view of the entire thorax. Cx, coxa; Epm$_2$, Epm$_3$, epimera of meso- and metathorax; Eps$_1$, Eps$_2$, Eps$_3$, episterna of pro-, meso-, and metathorax; F, femur; iS, sternum of first abdominal segment; iiSp, iiiSp, spiracles of second and third thoracic segments; L, lateral lobes of the metasterna; PN, pronotum; S, a suture; S$_1$, S$_2$, S$_3$, pro-, meso-, and metasterna; Sa, invaginations of sternal apodemes (furcae); 1Sp, first spiracle of abdomen; T, tympanum; Ta, tergum of mesothorax; Tar, tarsus; Tb, tibia; Te, tergum of first abdominal segment; Tg, tergum of metathorax; Tr, trochanter; W, cut end of wings; WP, wing processes.

organs of flight. In the Diptera, where only the mesothoracic wings are present, the mesothorax (Fig. 53) is greatly enlarged and appears to occupy the entire thoracic region.[2] In the Culicidae the thorax is distinctly wedge-shaped, the thick part of the wedge occupying the dorsal surface. The prothorax is greatly reduced. The pronotum is represented by two sclerotized areas on each side (Fig. 53 PN,PPN) the anterior pair being joined by a narrow membrane lying in front and somewhat beneath the mesonotum. The posterior pronotum has generally been called the proepimeron and probably corresponds to the humeral callus of the higher Diptera. The pleuron consists of a small episternum as in the grasshopper. The mesothorax occupies the greater part of the thorax. The mesonotum (Mes) extends from the head to the scutellum (Sc) and appears to occupy the entire dorsal surface. The scutellum (Sc) belongs to the mesothorax and is separated from the mesonotum by a distinct suture. Viewed from the dorsal surface it is trilobed and each lobe bears a distinct group of bristles. Directly behind and below the scutellum is a large, smooth, chitinized area, the postnotum (P). The side of the thorax is largely made up of the mesopleuron. It begins directly in front of the mesothoracic spiracle (iiSp) and extends to the suture cephalad of the metathoracic spiracle (iiiSp). Unlike that of the grasshopper, the episternum in the flies is divided into two distinct parts, the so-called mesanepisternum and the meskatepisternum. The latter sclerite is generally called the sternopleuron in all the Diptera. The mesepimeron is a large, rectangular-shaped sclerite. Behind it lies the metathorax, greatly reduced in size and united rather firmly to the abdomen. The metanotum (N) appears as a very narrow band lying behind the postnotum and articulating with the tergum of the first abdominal

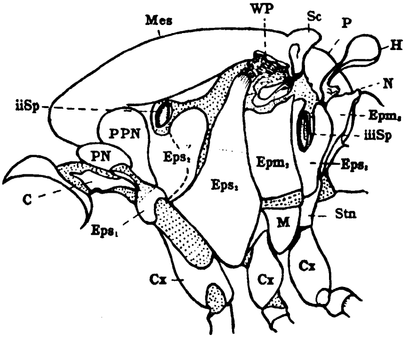

Fig. 53. Lateral view of the thorax of a mosquito (*Psorophora* sp.). C, cervical slcerite; Cx, coxa; Epm$_2$, Epm$_3$, epimera of the meso- and metathorax; Eps$_1$, Eps$_2$, Eps$_3$, episterna of the pro-, meso-, and metathorax; H, haltere; iiSp, iiiSp, spiracles of meso- and metathorax; M, meron; Mes, mesonotum; N, notum of metathorax; P, postnotum of mesothorax; PN, pronotum; PPN, postpronotum; Sc, scutellum; Stn, sternum; WP, cut ends of wing.

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[2] The thorax of the various orders of insects treated in this work is discussed under the groups in later chapters.

segment. Laterally the metathoracic spiracle is found in the metepisternum, and directly behind this sclerite is the metepimeron, rather faintly delimited from it. Directly above the latter sclerite is found the haltere (H). Located above and between the coxae of the second and third pair of legs is the so-called meron (M).

In the mosquitoes, as in nearly all the Diptera, the pleural sclerites bear groups of hairs or spines that are of great taxonomic significance. For an account of the pilotaxy, see pages 256–258.

The Appendages of the Thorax

THE LEGS (Fig. 54): Each segment of the thorax bears a pair of legs. Each leg is articulated to the thorax by its basal segment, the coxa, located in the membranous area between the pleural plates—the episternum and epimeron and the adjacent parts of the sternum. An insect's leg consists of five distinct parts:

The coxa (Cx) varies greatly in size and shape in different insects. It may be firmly attached to the body wall or very movable, as in the housefly and grasshopper.

The trochanter (Tr) is a small segment of varying shape and forms the attachment point for the next segment, the femur.

The femur (F) is usually an elongated segment and may be greatly enlarged as in jumping and leaping insects; e.g., grasshoppers and fleas.

The tibia (Tb) is usually slender, nearly always as long or longer than the femur, and frequently bears many stout hairs or spines. The tip may be armed with special spines.

The tarsus (Tar) is generally divided into segments, five being the most common number. There may, however, be only one segment as in the lice, two in plant lice, three in some grasshoppers, etc. The first segment is frequently greatly elongated and has been called the metatarsus. Some of the segments may be heavily armed with spines or stout setae. The last segment is generally provided with a pair of claws (Fig. 54 C). The claws arise from a special elongation of the last joint. The claws are frequently modified and adapted for various purposes and are moved by rather powerful retractor muscles. In some groups, as the lice, and some Mallophaga, there is only a single claw, which is adapted for clinging to hairs. The claws may be simple, toothed, equal in size, or one claw may be much larger than the other.

On the ventral surface of the claws and attached to the membrane of the last tarsal segment is a pair of membranous pads, the pulvilli (Fig. 54 P). Each pulvillus may be provided on its ventral surface with numerous, glandular hairs, the so-called tenent hairs. It is by means of these tenent hairs (each one is connected with a gland) that flies are enabled to walk on ceilings, glass, and other smooth surfaces. The sticky excretion gathers up all sorts of bacteria, spores, cysts, and filth and distributes them. Between the pulvilli and below them is a long, narrow, hairy spine, the empodium (E). The empodium varies greatly in different insects. It may be hairlike, it may be a stout spine, or it may be padlike and then it is said to be pulvilliform.

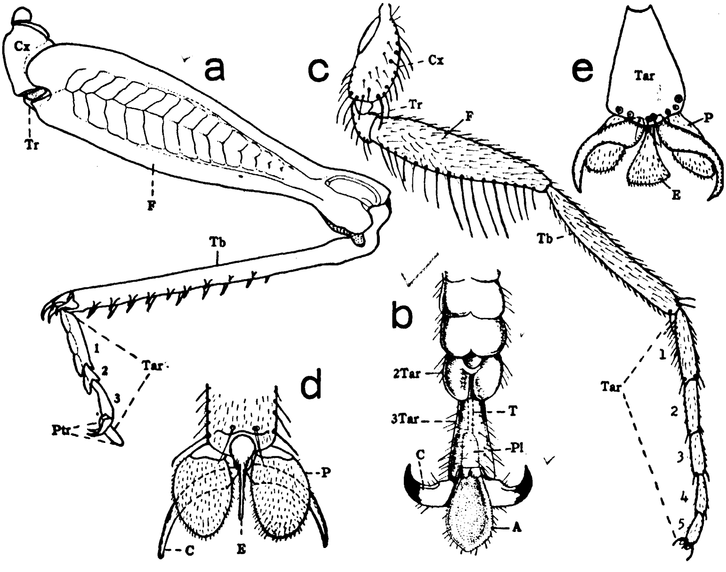

Fig. 54. The legs of insects. (*a*) Hind leg of a grasshopper. (*b*) Tarsus and pretarsus of leg of grasshopper. (*c*) Leg of housefly (*Musca domestica*). (*d*) Pretarsus of housefly. (*e*) Tip of tarsus and pretarsus of fly (*Stratiomys*). A, arolium; C, claw; Cx, coxa; E, empodium; F, femur; P, pulvillus; Pl, unguitractor plate; Ptr, pretarsus; T, tendon of muscle attached to unguitractor plate; Tb, tibia; Tar, tarsus; Tr, trochanter.

THE WINGS: Probably the most important appendages of the thorax are the wings. They are not true appendages but are outgrowths from the dorsolateral margins of the meso- and metathorax.

In insects with incomplete metamorphosis, as the Orthoptera and Hemiptera, the external development of the wings may be easily observed. In holometabolous insects, as the Diptera, Lepidoptera, and other orders, the wings are developed internally during the larval growth and only become exposed as the wing pads at the time of pupation.[3] The great majority of insects possess two pairs of wings, though the Diptera have only one pair, the metathoracic wings being represented by the halteres or balancers, vestiges of what may have been originally wings (Fig 53 H). Some orders are wingless, as the Anoplura (lice) and Siphonaptera (fleas), though they undoubtedly descended from winged ancestors. The Apterygota consists of two or three orders in which the wingless condition is primitive.

The wing as seen in an adult insect consists of two fused membranes. The longitudinal thickenings, the veins (Fig. 55), are more heavily chitinized areas laid down around the cavities through which tracheae supplied the developing wings with air. The complete system of veins in a wing is called

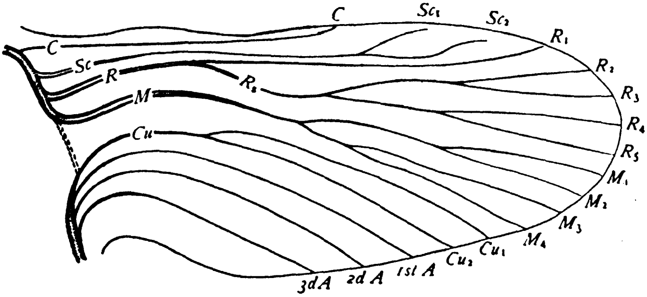

Fig. 55. Hypothetical tracheation of a wing of a primitive nymph. (After Comstock.)

its venation or neuration. The venation presents excellent characters in systematic work, and various systems of naming these veins have developed in each order. Comstock and later Comstock and Needham developed what they called the hypothetical type of venation (Fig. 55) of a primitive winged insect. As all winged insects are believed to have descended from a common ancestor, many extensive studies have been carried on to interpret the venation of the wings in the various orders. As a result of Comstock and Needham's work, a uniform system of naming the veins was evolved, though unfortunately it has not been adopted by all taxonomic workers. In fact, there are many systems and each author follows his own bent in naming the veins. In medical entomology it is necessary to have a thorough knowledge of the venation in the Diptera, and the discussion here is largely restricted to that order.

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[3] For a full account of the development of wings and wing venation, consult Comstock (1918, 1947) or Imms (1934).

The principal veins in an insect's wing consist of a series of longitudinal veins and a few definite cross veins. Modification of the hypothetical type takes place through addition or reduction, mainly, reduction in the dipterous wing. Reduction occurs through fusion of veins or their loss. These modifications are differently interpreted by various workers so that uniformity cannot be looked for in taxonomic work. The arrangement of the veins and cross veins in the hypothetical type is shown in Fig. 55. The following table gives the nomenclature of the veins according to the Comstock-Needham system and to the system used extensively by the students of the Diptera.

Terminology of dipterists	*Comstock-Needham terminology*	*Abbreviations*
Costal	Costa	C
Auxiliary vein	Subcosta	Sc
1st longitudinal vein	Radius one	R_1
2nd longitudinal vein	Radius two and three	R_2 and R_3
3rd longitudinal vein	Radius four and five	R_4 and R_5
4th longitudinal vein	Media one Media two	M_1 and M_2
5th longitudinal vein	Media, 3rd, and Cubitus, or Cubitus alone	M_3 and Cu, or Cu
6th longitudinal vein	Anal veins	1A, 2A, 3A

Figs. 56 and 57 present the wing of a *Tabanus* species with the veins and cells labeled according to the Comstock-Needham system and that commonly used by dipterists.

The costa (C) is the thickened frontal margin of the wing; the anterior border is generally called the costal border.

The subcosta (Sc) is directly behind the costa and parallel to it; it is generally known as the auxiliary vein (Fig. 57 a) by dipterists. In the Diptera the subcosta is rarely branched.

The radius lies directly behind the subcosta and, in the hypothetical type, is five-branched. In *Tabanus* the radius is four-branched, R_3 having been lost by fusion with R_2. The first branch, R_1, is simple and corresponds to the first longitudinal (Fig. 57 1st). Near the base of the wing a short branch, the radial sector (Fig. 56 Rs), arises, which divides into two branches, the posterior branch again dividing. The first branch constitutes the 2nd longitudinal vein (Fig. 57 2nd); the posterior branch with its two divisions is the 3rd longitudinal vein.

The media extends through the middle of the wing. In *Tabanus* it is three-branched (Fig. 56 M_1, M_2, M_3). The first two branches constitute the 4th longitudinal vein (Fig. 57 4th).

The cubitus is typically two-branched and with the posterior branch of media (M_3) constitutes the 5th longitudinal vein (Fig. 57 5th).

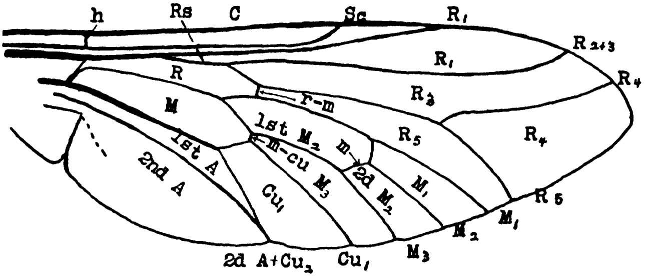
h
Rs
C
Sc
R_1
R_{2+3}
R_1
R_4
R
R_3
M
r-m
R_5
R_4
1st M_2
m
1st A
m-cu
2d A
Cu_1
M_3
2d M_2
M_1
R_5
M_1
M_2
2d A+Cu_2
Cu_1
M_3

Fig. 56. Wing of *Tabanus* sp. with the veins and cells labeled according to the Comstock-Needham system.

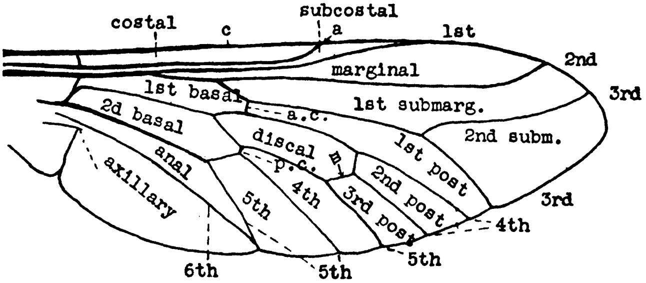
costal
c
subcostal
a
1st
2nd
marginal
3rd
1st basal
2d basal
1st submarg.
a.c.
2nd subm.
discal
1st post
anal
m
2nd post
p.c.
axillary
4th
5th
3rd post
3rd
4th
5th
6th
5th

Fig. 57. Wing of *Tabanus* sp. with the veins and cells labeled in accordance with the system followed by students of the Diptera (flies).

The anal veins are the two or three veins (1st, 2nd, and 3rd when present) lying behind the cubitus. In the Diptera the first anal vein is greatly reduced or absent. It is frequently represented by a furrow, the anal furrow, which is close behind the cubitus. The second anal vein is well preserved (Fig. 56 2d A) and corresponds to the 6th longitudinal (Fig. 57 6th).

The cross-veins include several well-marked veins. These are (1) the humeral (h), (2) the radio-medial (r-m), known also as the anterior cross-vein (ac), and (3) the medio-cubital (m-cu), commonly called the posterior cross-vein (discal cross-vein of Williston; Fig. 57 pc). The radio-medial or anterior cross-vein is very constant, and its location will always give a clue to the venation of the wing. Another important cross-vein is the medial (m).

The areas of the wings bounded by veins are called cells. In the Comstock-Needham nomenclature the cell takes the name of the vein lying immediately in front of it (Fig. 56). In the older system the names of the cells are rather arbitrary, and it is at times difficult to interpret an author's work unless he is very specific in his explanations (Fig. 57).

THE ABDOMEN

The abdomen constitutes the third region of the body (Fig. 58). It is composed of a series of segments that retain the rather primitive annular form.

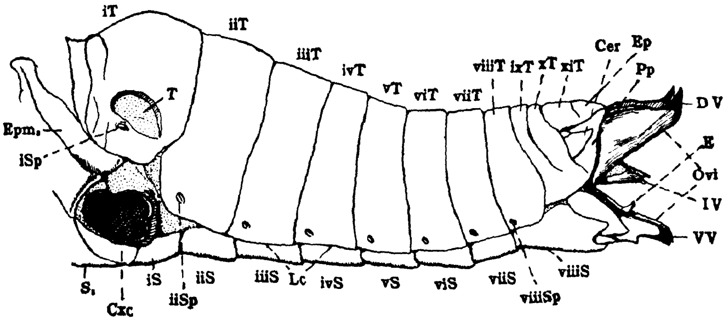

Fig. 58. Lateral view of the abdomen of a grasshopper (*Melanoplus differentialis*). Cer, cercus; Cxc, coxal cavity; E, egg guide; Ep, epiproct; Epm$_3$, epimeron of 3rd thoracic segment; Lc, lateral commisure; Ovi, ovipositor consisting of the dorsal valves (DV), ventral valves (VV), and inner valves (IV); Pp, paraproct or podical plate; S$_3$ sternum of third thoracic segment; iS–viiiS, first to eighth abdominal sterna; iSp–viiiSp, one to eight spiracles; iT–xiT, one to eleven tergites or terga; T, tympanum.

Each segment has a large tergum and a well-developed sternum. The pleural region is nearly always membranous, though differentiated sclerites may sometimes occur. When the abdomen of a grasshopper is examined, it will be observed that the terga and sterna closely approach each other while the pleurum is represented by a folded membrane, the longitudinal conjunctiva. The abdomen consists of eleven segments, the last three or four being modified to form, with the modified appendages, the clasping organs of the male or the ovipositor of the female (genitalia). Though eleven segments are considered the primitive number, it is often difficult to recognize more than eight or even less. This is due to their reduction or modification in the higher orders such as the Diptera and Hymenoptera.

The terminal segments with their appendages are highly modified in many insects to form, in the males, the most bizarre types of clasping organs. As the parts entering into the external genitalic structures have not been homologized throughout the various orders, it does not seem worth while to discuss them as they occur in the more generalized groups. These structures will be dealt with in some detail in those groups that are of importance from the standpoint of medical entomology.

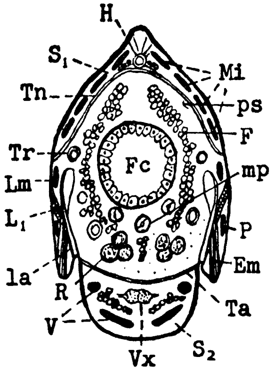

Fig. 59. Diagrammatic cross section of the third segment of the abdomen of a grasshopper to show position of muscles and some of the internal organs. Em, external lateral muscles; F, fat body; Fc, food channel or alimentary canal; H, heart; L_1, internal lateral muscle; la, lateral apodemes of sternum; Lm, lateral internal dorsal muscle; Mi, median internal dorsal muscles; mp, Malpighian tubules; P, an external muscle; ps, perivisceral sinus for blood; R, reproductive organs; S_1, S_2, dorsal and ventral sinuses; Ta, ventral diaphragm; Tn, dorsal diaphragm; Tr, trachea; V, ventral muscles; Vx, ventral nerve cord. (Modified from Snodgrass.)

INTERNAL ANATOMY

The internal anatomy of insects can be referred to only briefly. Those structures that chiefly interest the medical entomologist will be outlined in brief detail, i.e., the digestive system and its appendages, the respiratory system, the blood, the muscular system, and the reproductive system.

THE DIGESTIVE SYSTEM AND ITS APPENDAGES

The most striking feature of an insect is that the body wall (Fig. 43) forms the skeleton, giving support and protection to the internal organs. The body wall may represent the wall of a cylinder. The alimentary canal occupies a more or less central position in the cylinder and connects the mouth opening with that of the anus. It may be barely as long as the body or it may be coiled and doubled on itself, making several convolutions. Above it lies the heart, and the nerve chain is ventral (Fig. 59). The digestive system is composed of the following parts: (1) fore-intestine, (2) mid-intestine, (3) hind-intestine, (4) salivary glands, (5) Malpighian tubules, and (6) accessory glands (Fig. 60).

FORE-INTESTINE: The fore-intestine begins at the rear of the buccal cavity. Its anterior end is a rather wide-open channel into which the food is passed after mastication. This leads directly into the pharynx, which, in mandibulate insects, is a thin-walled tube. In insects with piercing mouth parts the pharynx is an organ of suction and is provided with powerful muscles. By the contraction of these muscles the pharynx acts as a pumping organ (Fig. 60). The pharynx leads into the esophagus, a thin-walled tube, which may terminate in a crop, followed by a proventriculus or gizzard. In most of the bloodsucking Diptera the gizzard is reduced to a valve that opens into the mid-intestine. In addition to these structures the esophagus may have one to three diverticula or food reservoirs (Fig. 60), as they are called. These diverticula are very large in the mosquito but their exact function is not well known.

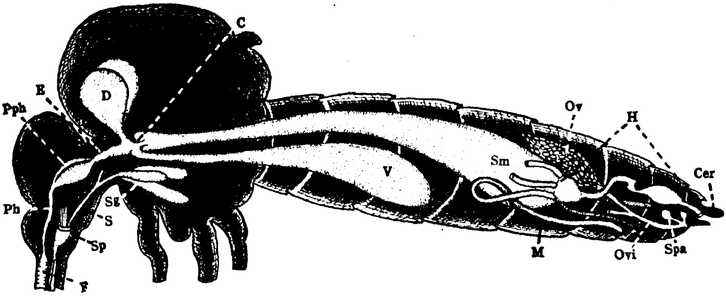

Fig. 60. Diagrammatic sectional view of the internal structures of a female mosquito. C, cardiac or esophageal valve; Cer, cercus; D, dorsal diverticula; E, esophagus; F, food channel; H, hind-intestine; M, Malpighian tubules; Ov, ovary; Ovi, oviduct; Ph, pharynx; Pph, pharyngeal pump; S, salivary duct; Sg, salivary glands; Sm, stomach; Sp, salivary pump; Spa, spermatheca; V, ventral diverticula of esophagus.

THE MID-INTESTINE: The mid-intestine or stomach (Fig. 60) extends from the proventriculus to the insertion of the Malpighian tubules. It may be short and saclike or it may be long and coiled. It is in this portion of the alimentary tract that digestion and most of the absorption take place. The mid-intestine is joined, in many cases, to the fore-intestine by what has been termed the esophageal valve (Fig. 60 C). The esophageal valve is absent in the lice (Anoplura) and the bedbug. In many insects the food contained in the mid-gut is surrounded by a delicate membrane, the peritrophic membrane, which originates from a group of cells, the cardiac cells, located at the juncture of the epithelium of the fore- and mid-intestine. The peritrophic membrance is present in the majority of insects.[4]

THE HIND-INTESTINE: The origin of the hind-intestine is marked by the insertion of the Malpighian tubules. In many insects the hind-gut is divided into three fairly well defined regions—the ileum, the colon, and the rectum (Fig. 61).

STRUCTURE OF THE INTESTINE: The fore- and hind-intestine are of ectodermal origin. Internally each is lined with a thin intima, which is continuous with the cuticula of the body wall. The intima may be very thick as in the gizzard (proventriculus). Beneath the intima is a single layer of epithelial cells that is continuous with the epidermis. A basement membrane underlies the epithelial cells. The fore-intestine is surrounded by a layer of longitudinal muscle fibres overlaid by a thin band of circular muscle fibers. In the hind-intestine the muscle layers, from within, are first circular, then longitudinal, and usually again circular. The mid-intestine is of entodermal origin. It lacks the internal lining of intima and is composed of a single layer of epithelial cells resting on a basement membrane. It is surrounded by a layer of circular muscles overlaid by a thin sheet of longitudinal fibers. The entire intestine outside the muscle layers is surrounded by a thin sheet known as the peritoneal membrane. The peritoneal membrane may then be considered as the inner lining of the body cavity or hemocele.

THE SALIVARY GLANDS: These are the most important glands connected with the fore-intestine, and they often play a significant role in the transmission of parasites (Figs. 60–62). The glands are paired structures and lie on each side of the intestine in the hemocele. Each gland consists of a cellular part and a duct that unites with its fellow from the opposite side to form a common salivary duct. The common duct opens at the base of the hypopharynx and, in some of the bloodsucking insects, extends throughout its length (Fig. 97). These glands vary greatly in size and complexity. In the mosquito the glands are quite large and occupy a considerable space in the thorax. Each gland of the mosquito is trilobed, with a central gland and two lateral glands (Fig. 62). The ducts of the three glands from each side unite into one, and this in turn joins its fellow from the opposite side to form a common salivary duct. At its point of entrance into the hypopharynx there is a muscular pump that forces the secretion into the wound made at the time

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[4] Wigglesworth (1930) states that it is absent in the Hemiptera, adult Lepidoptera, and some Coleoptera.

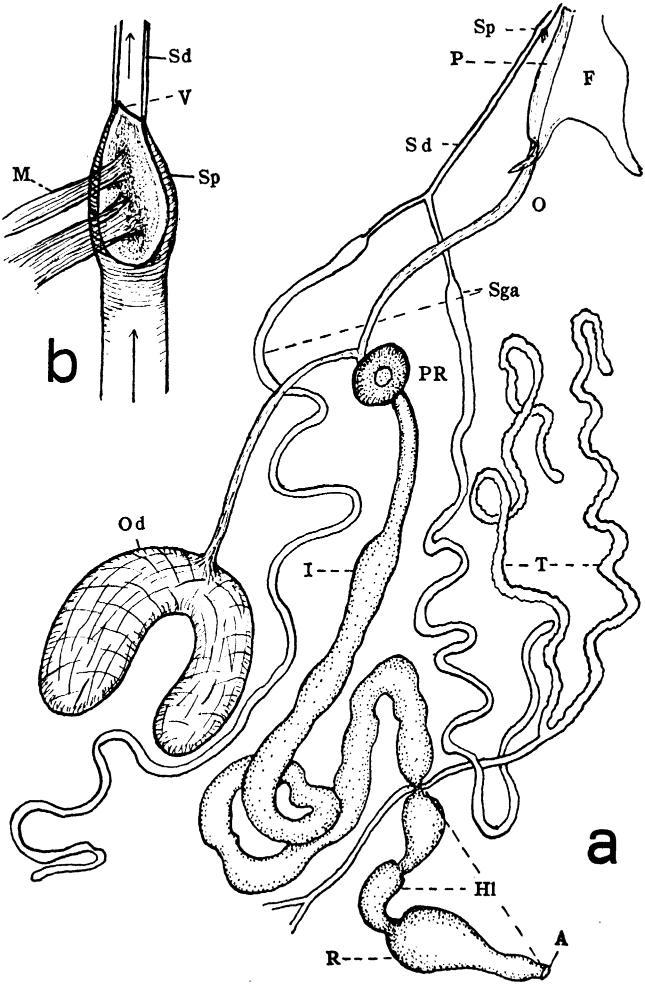


Fig. 61. (*a*) The digestive tract of the housefly with the main parts labeled. (*b*) The salivary syringe to show details (highly magnified). A, anal opening; F, fulcrum in head of fly; HI, hind-intestine; I, mid-intestine extending from proventriculus (PR) to insertion of Malpighian tubules (T); M, muscles to syringe; O, esophagus; Od, esophageal diverticulum or crop; P, pharynx; PR, proventriculus; R, rectum; Sd, salivary duct leading to hypopharynx from salivary syringe; Sga, salivary glands; Sp, salivary syringe; T, Malpighian tubules; V, valve to prevent backflow of salivary fluid.

of obtaining blood. In many insects the salivary glands function for the secretion of silk, as in the caterpillars and the larvae of many Hymenoptera.

The functions of the secretion of the salivary glands of bloodsucking insects are not well understood. It is known that in the mosquito the secretion is injected into the wound, causing the irritation and swelling. How this is brought about is not known. In some insects the secretion possesses an anticoagulin (*Anopheles rossi* and *A. jamesii*), but in others such a function has not been demonstrated. Metcalf (1945) has shown that the salivary glands of *Anopheles quadrimaculatus* contain an anticoagulin that is thermostable and active at dilutions of 1:10,000; they also contain a powerful agglutinin for most vertebrate blood but not for chicken or turtle blood. Cornwall and Patton have shown that the saliva of a muscid (*Musca crassirostris*) contains a powerful anticoagulin, whereas *Stomoxys calcitrans* (the stable fly) has no anticoagulin. Lester and Lloyd find that the salivary secretions of *Glossina* flies possess a powerful anticoagulin. Yorke and Macfie report that the salivary secretion of *Anopheles maculipennis* agglutinates red blood cells and also

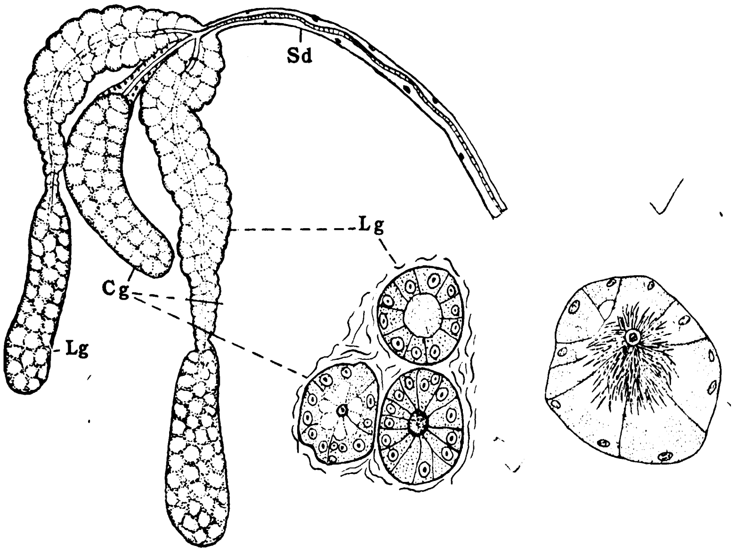


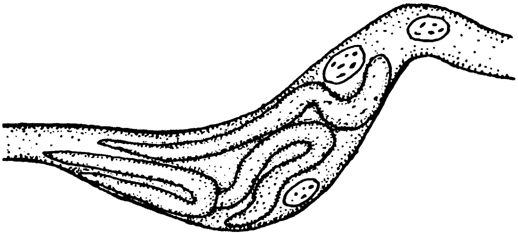
Fig. 62. Left: The left half of the salivary gland of *Anopheles punctipennis. Center:* Cross section of the glands. *Right:* Cross section of a gland from *Culex pipiens* showing masses of sporozoites of bird malaria. Cg, central gland; Lg, lateral gland; Sd, salivary duct.

possesses an anticoagulin and that the secretions of *Culex pipiens* and *Aedes aegypti* do not possess an agglutinin nor do they contain an anticoagulin. McKinley determined that an emulsion of the glands of *Aedes aegypti,* when injected intradermally, caused a severe itching and characteristic wheals on susceptible persons; it does not possess an anticoagulin nor does it hemolyze blood. It has also been shown that some species of horseflies (Tabanidae) possess an anticoagulin in their salivary glands. Puri has shown that the saliva of the bedbug causes the severe irritation and that it contains an anticoagulin. As bloodsucking insects must ingest their blood meal through a very minute channel, it would seem essential that some agent or agents be present to prevent the coagulation of the blood here or in the esophagus in order to allow it to flow freely into the mid-gut where digestion takes place.

THE MALPIGHIAN TUBULES: The Malpighian tubules (Figs. 60,61) are usually elongated tubes that arise at the junction of the mid- and hind-intestine. In their origin they belong to the hind-gut. Their number varies but they generally occur in multiples of two, the usual number being four or six. In the Culicidae there are five, but most of the Diptera possess four. Each Malpighian tubule arises at the anterior end of the hind-gut and terminates blindly in the hemocele. Though they are usually single, branching may occur or two may unite to form a common opening into the intestine (Fig. 61). In structure each tube is composed of a ring of epithelial cells surrounding a central channel. Each cell possesses a prominent nucleus, which may be much branched. The epithelial layer of cells rests on a basement membrane surrounded by a delicate peritoneal sheath. The function of these tubules is now generally regarded as excretory, extracting waste from the blood and storing it in the cells or passing it to the hind-intestine. The Malpighian tubules are of great interest to the parasitologist because within them certain parasites undergo part of their life cycles, for example, *Dirofilaria immitis* (Fig. 63), a filarial roundworm infecting the dog.

THE RESPIRATORY SYSTEM

The respiratory system of insects consists of a paired series of tubes, tracheae, which, by branching, ramify through all parts of the body and its appendages. These tubes arise as invaginations of the body wall and are usually located on the pleura of the second and third thoracic and first eight abdominal segments (Fig. 42). The external openings are called spiracles, and the usual number is ten pairs. The spiracle is usually surrounded by a chitinous ring, the peritreme, and opens into an atrium or air chamber. From the air chamber extends a trachea, which branches and unites with its fellows to form longitudinal and transverse connections. From these main trunks innumerable branches extend to all the tissues and organs of the body. The spiracle, in its simplest form, consists of an opening to the exterior to admit air. There is, however, extreme variation in the structure of spiracles, and many possess a rather complicated apparatus for closure and for excluding dust, dirt, and moisture. In many insects a single spiracle may have several openings (Fig. 194). The trachea consists of a tube lined internally with intima arranged in such a way that the thickenings form a spiral (Fig. 64). These spiral thickenings (taenidia) keep the trachea distended and allow the free passage of air.



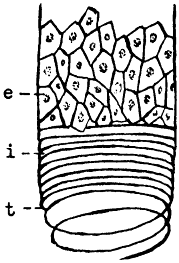


Fig. 63 (*left*). Malpighian tubule from *Aedes vexans* (a mosquito) containing three larval filarial worms, *Dirofilaria immitis* (dog filaria). These developed 17 days after the mosquito fed on the blood of a dog containing microfilaria.

Fig. 64 (*right*). Small section of a trachea to show structure. e, epithelium; i, intima; t, taenidia.

The tracheae finally terminate in tracheoles, which are the essential organs for respiration. The tracheoles are minute tubes that lack a chitinous lining and penetrate the various tissue cells to furnish the needed air.

In addition to the respiratory system described above, various modifications are found. In aquatic insects there may be tracheal gills, as in mosquito larvae (Fig. 105), and blood gills (which are rare), as in the larvae of some species of *Chironomus* and *Simulium.*

In order to indicate the distribution of spiracles the following classification is much used (mostly applied to dipterous larvae):

1. *Holopneustic*—Spiracles all open and arranged on thorax and first 7 or 8 abdominal segments.
2. *Hemipneustic*—One or more spiracles closed.
    (1) *Peripneustic*—Usually spiracles of wing bearing segments closed.

(2) *Propneustic*—Only first pair of thoracic spiracles open. Example: pupae of mosquitoes.
(3) *Metapneustic*—Only the last pair of spiracles is open. This type is found in mosquito larvae, some parasitic larvae as *Hypoderma* spp. (warble flies), and others.
(4) *Amphipneustic*—The first and last pair of spiracles are open. Example: larvae of the Muscidae.

THE BLOOD

The blood is generally a colorless fluid that circulates freely in the hemocele, bathing directly all the internal organs and tissues. In some insects it may be colored from the absorbed food substances or may contain hemoglobin (rare). In the plasma are found several types of leucocytes, but their functions are not well known. One type possesses a phagocytic function, and these cells undoubtedly play an important role. The blood is kept in circulation by a dorsal pumping organ, the heart. The heart is a tube that extends from near the caudal extremity to the head. It is usually closed at the posterior end and terminates in a nonpulsating anterior vessel, the aorta. In the heart there are paired ostioles or openings. The pulsations of the heart travel from behind forward so that the blood flows in at the ostioles and is then forced cephalad by the wavelike muscular contractions, being discharged through the aorta. The ostioles are so constructed that they admit the entry of the blood, but as the contraction waves passes forward, backflow in the heart itself and to the hemocele is prevented.

THE MUSCULAR SYSTEM

The muscles of insects are all internal. The body wall and various invaginations (apodemes, furca, etc.) furnish the points of origin, and the insertion points are those portions or parts of the body to be moved. As a rule, insect muscles are composed of numerous fibers enclosed in sheaths and appear almost colorless, transparent, or yellowish white; they are soft and gelatinous. The number of muscles is large and their arrangement very complicated. In their histological structure all the muscle fibers are cross-striated and present a beautiful appearance to the microscopist. To the parasitologist and medical entomologist the normal histology is of considerable significance, for in some muscle tissues certain Nematodes pass part of their life cycle (*Wuchereria bancrofti,* in the thoracic muscles of the mosquitoes; *Loa loa* in similar muscles of Tabanidae).

THE REPRODUCTIVE SYSTEM

In practically all insects the sexes are distinct. The female reproductive organs (Fig. 65) consist of the ovaries, paired structures; each ovary is composed of a variable number of egg tubes or ovarioles; the ovarioles from each side open into an oviduct; the oviducts unite to form a common duct, the vagina, which opens to the exterior ventral of the anal opening. Attached to the vagina and opening into it are usually found a pair of accessory glands and a pouch (there may be several), the spermatheca, for the reception and storage of the sperm. As the majority of insects probably mate but once, and the female oviposits over a long period of time, it is essential that a storage place be provided for the sperm.

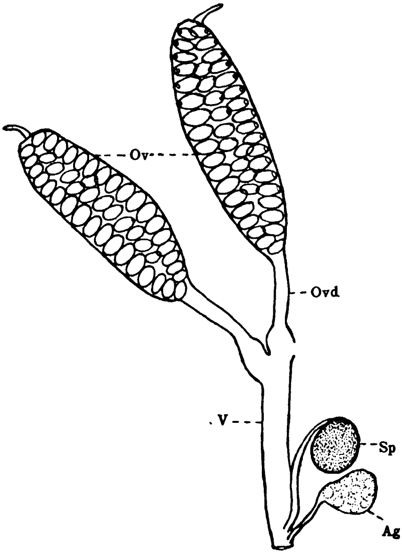


Fig. 65. Female reproductive system of *Anopheles punctipennis.* Ag, accessory gland; Ov, ovary; Ovd, oviduct; Sp. spermatheca; V, vagina.

The male reproductive organs consist of a pair of testes composed of testicular follicles; from each testis extends a canal, the vas deferens, which unites near the exterior with its fellow to form the ejaculatory duct. Usually each vas deferens is enlarged along its course to form a sac, the vesicula seminalis, in which the spermatozoa congregate. There is also generally a pair of accessory glands. The ejaculatory duct, at its terminal section, is enclosed in a chitinous tube that forms the intromittent organ or aedeagus. The aedeagus or penis is a variable structure, and around it often develop a most complicated grouping of clasping and holding organs.

THE METAMORPHOSIS OF INSECTS

The great majority of insects, in the course of their postembryonic development, undergo remarkable changes in form or metamorphosis; the beautiful butterfly was once a caterpillar; the May beetle, a grub; the housefly, a footless maggot. The most obvious changes are external, though the internal metamorphosis is even more complicated and as yet not well understood. Practically all insects lay eggs and these develop externally to the mother. In some insects the embryonic development may be completed before the egg is laid, as in many plant lice and flesh flies; the egg may hatch and the larva develop in a uterinelike cavity in the mother, as in the Glossina flies, the sheep tick or ked, and all the *Pupipara;* or partial embryonic development may take place before egg laying, as in the bedbug. There are two general types of postembryonic development—incomplete metamorphosis (hemimetabolous), and complete metamorphosis (holometabolous). Those insects that do not undergo changes in form during growth are called ametabolous (these include the two primitive orders, Thysanura and Collembola).

THE EGG: The eggs of insects vary greatly in their shape, size, and markings. Attention here is directed only to the eggs of those insects that are annoying to man or his domestic animals. These eggs all possess a distinct shell and are laid on or near the food on which the young are to feed. The egg of the bedbug (Fig. 71) is quite large and distinctive; that of the louse is attached to hairs or clothing and possesses a structure for attachment (Fig. 81); the housefly deposits large, smooth, white eggs (Fig. 173). Frequently the most distinguishing characteristic of the eggs of certain insects is the manner of oviposition. Thus the mosquito, (*Culex* spp., lays its eggs in rafts (Fig. 111) on the surface of the water; horseflies (Tabanidae) deposit their eggs in masses glued to the leaves or stems of aquatic or semiaquatic plants (Fig. 158).

The young larva escapes from the egg either by breaking the shell with its mandibles or mouth hooks, by pushing off a cap by means of an air cushion (lice); or by breaking the shell with a special apparatus known as an egg burster or hatching spines. Such hatching spines are easily seen on the dorsal surface of the head of the first-stage mosquito larva.

INSECTS WITH INCOMPLETE METAMORPHOSIS: The most striking feature of this type of metamorphosis is the development of wings as external outgrowths of the mesothoracic and metathoracic segments. In all other respects except in size and the rudimentary condition of the genital appendages, the young (generally called nymphs) resemble the adults. A good example is a grasshopper or a bug. Furthermore in this type of metamorphosis the life of the young and of the adult is essentially the same: they live in the same situation and feed on the same food.[5] The adults are provided with wings giving them increased power of locomotion. The power of flight gives them a wider feeding range and provides for the more rapid spread of the species and more successful mating.

INSECTS WITH COMPLETE METAMORPHOSIS: In this group the young and adults are totally unlike in appearance. Familiar examples are the caterpillars, which develop into moths or butterflies; maggots, which later become flies; and grubs, which transform to beetles. The young stage is generally known as the larva. When the larva has reached maturity, it ceases to feed and proceeds to undergo a most remarkable change. It now either spins a silken cocoon (most moths), forms a cell in the ground (many beetles), seeks out some sheltered place, uses the last larval skin as a shelter (many Diptera), attaches itself to some support (butterflies and some beetles), or in other ways makes provision for the changes that are to follow. The last larval skin is now cast off (except in many Diptera), and a new stage, the pupa, appears (Fig. 103). Within the pupa many of the larval tissues are broken down and rebuilt to form the adult. From the pupal skin emerges an entirely new form, the adult.

The most striking characteristics of this type of metamorphosis are: (1) the larval stage occupies an entirely different habitat and requires different food from that of the adult; (2) the wings are developed internally during the larval period and only appear externally as wing pads (Fig. 103) in the pupal stage; and (3) a resting stage appears, the pupa, within which the larval tissues are broken down and the adult is rebuilt from histoblasts or embryonic tissues.

GROWTH IN INSECTS

The growth period in insects is restricted to the nymphal or larval stage. Growth in the nymphal and larval stages is accomplished by a periodic shedding of the skin, molting. As the skeleton is external, no increase in size beyond a certain expansion can take place after the cuticula has hardened. This difficulty is overcome by molting. When a larval stage has reached its full growth, the cuticula splits at some convenient place and a new larva crawls out provided with a soft external skin capable of considerable extension. The new cuticula is laid down beneath the old before the latter is shed. Molting takes place at regular intervals and the number of molts varies in different groups of insects. In the mosquito the larva molts four times before the pupal stage is reached; in most of the higher Diptera only three molts occur; in the beetles and moths five or more may occur; in other groups three to many molts may take place.[6] During the larval growth large quantities of food are stored up as fat. This food supply is largely used up during the pupal period, being employed in the development of the tissues of the adult.

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[5] This last statement does not apply to three orders, the May flies, stone flies, and the dragonflies, whose nymphs are aquatic and adults aerial. Comstock has designated this type as incomplete or hemimetabolous, and the type represented by the Orthoptera, Hemiptera, Anoplura, etc., as paurometabolous or gradual metamorphosis.

The adult, though it feeds, does not increase in size. Molting does not occur, and, once the external skeleton is fully hardened, no great expansion of body size is possible. Food is now taken to provide for the adult activities and the development of eggs and sperm. In many insects the adults do not feed but depend on the store of food carried over from the larvae.

SYNOPSIS OF INSECT CLASSIFICATION

The Hexapoda or insects constitute an immense assemblage of species; probably more than 800,000 species have already been described, and new ones are constantly being discovered. The class is divided into two subclasses, the Apterygota and Pterygota. The Apterygota contain the wingless, primitive insects, and these are included in two orders, the Thysanura and the Collembola. The Pterygota include all the other insects whether wingless or not. The wingless condition of the forms included here is not a primitive one but acquired. The Pterygota are divided into a number of orders but rarely do workers agree as to the exact number or their arrangement. It is proposed here to give a brief synopsis of only those orders that contain important species annoying to man or his animals.[7] These include only eight or nine of the twenty to nearly forty orders now recognized. Of these orders the most important are the Hemiptera, the Anoplura, the Diptera, and the Siphonaptera. The other orders, the Orthoptera, Lepidoptera, Coleoptera, and Hymenoptera, contain forms that may act as mechanical carriers of disease organisms

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[6] The intervals between molts or ecdyses are called stadia; the form of the larva or nymph during a stadium is called an instar.

[7] For a full account the reader is referred to works by Comstock, Sharp, Imms, Kellogg, Brues and Melander, and Matheson, all indicated in the References.

(Orthoptera), produce diseased conditions by their poisonous hairs (Lepidoptera) or stings (Hymenoptera), cause ill effects by their vesicating substances (cantharidin of blister beetles), or serve as intermediate hosts of helminths (Coleoptera, Orthoptera, etc.). It is not proposed to treat these four orders in any detail, but they are discussed briefly in the last chapter and mentioned in a few other places. The following simple key will serve to place those insects that are of great importance to man:

KEY TO THE PRINCIPAL ORDERS OF INSECTS (ADULTS) OF MEDICAL IMPORTANCE

1. Wingless insects 2
   Winged insects 9
2. Free-living forms, not parasitic 3
   Not free-living, ectoparasites 5
3. Abdomen sharply constricted at base; cerci absent . . . . . . *Hymenoptera*
   Abdomen not sharply constricted at base, broadly joined to the thorax; cerci present or absent 4
4. Mouth parts fitted for biting; flattened insects; body without scales. (Many cockroaches) . . . . *Orthoptera*
   Mouth parts consisting of a proboscis coiled up beneath the head; body usually covered with scales or long hairs. (Wingless moths) *Lepidoptera*
5. Mouth parts formed for piercing and sucking 6
   Mouth parts adapted for biting. (Biting lice) . . (*Mallophaga*) *Anoplura*
6. Body strongly compressed (flattened from side to side); antennae in grooves visible from above; legs fitted for jumping or running. (Fleas) . . . . *Siphonaptera*
   Body not compressed but may be flattened from above down; antennae not in grooves, visible or not from dorsal surface 7
7. Antennae short, located in pits and not visible from dorsal surface. (Louse flies; Pupipara) . . . . *Diptera*
   Antennae fully exposed 8
8. Tarsus with one claw and fitted for clinging to hairs. (Sucking lice; Siphunculata) . . . . *Anoplura*
   Tarsus with two claws and not adapted for clinging to hairs . . *Hemiptera*
9. With a single pair of membranous wings; hind pair represented by short processes (halteres or balancers) . . . . *Diptera*
   With two pairs of wings 10
10. The two pairs of wings unlike in structure or texture 11
   The two pairs of wings similar in structure or texture 13

11. The front wings hard and horny, shell-like, and without distinct venation. Hind wings thin and membranous; mouth parts for chewing. (Beetles) . . . . *Coleoptera*
    The front wings not as described above 12
12. The front wings parchmentlike with a network of veins; hind wings folded fanlike beneath the front wings; mouth parts for chewing . . . . Orthoptera
    The front wings leathery at base and membranous on apical portion (Fig. 68); mouth parts fitted for piercing and sucking . . . . (*Heteroptera*) *Hemiptera*
13. Wings covered more or less densely with scales; mouth parts fitted for sucking and, when at rest, coiled up under the head . . . . . . *Lepidoptera*
    Wings not covered with scales; mouth parts fitted for biting or sucking but never coiled up under head 14
14. Mouth parts enclosed in a jointed beak and fitted for piercing and sucking; they are located at the posterior part of the head, just in front of the first pair of coxae . . . . (*Homoptera*) *Hemiptera*
    Mouth parts not enclosed in a jointed beak; in normal position . . . . *Hymenoptera*

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CHAPTER VI

The Orders Orthoptera and Hemiptera

THE order Orthoptera includes such insects as cockroaches, grasshoppers, crickets, and related groups. They possess chewing mouth parts (Fig. 45) and normally two pairs of wings, of which the outer (tegmina) pair is more or less parchmentlike with distinct veins; the lower or hind wings are thin and folded fanlike when at rest. Metamorphosis is gradual. Though the order contains many species that are destructive to vegetation (practically all are vegetarians), only a single family is of interest here.

THE FAMILY BLATTIDAE—THE COCKROACHES

Cockroaches are primarily inhabitants of the tropical and subtropical regions. They are easily recognized by their oval, flattened bodies; long, filiform antennae; and legs fitted for running or walking. The head is almost concealed by the prothorax and is bent downward so that the mouth parts project between the first pair of legs. Most of the species live in the wild in their natural habitats. At least four species, however, have become largely domesticated and have invaded our homes, restaurants, hotels, food-storage warehouses, commercial establishments of all kinds, and similar places where food and warmth are available. These species are all voracious feeders, attacking almost any vegetable or animal matter. They are largely nocturnal in activity, and warm kitchens, laundries, bakehouses, restaurants, and hotels are their favorite haunts. Unlike most insects the females produce special egg cases within their genital armature. When ready for egg laying the female excretes a special substance that forms an egg case (ootheca) composed of two parallel rows. As each egg sac is formed, an egg is passed into it either from the right or left ovary. This continues till a purselike capsule is completed. It may be seen extending from the end of the abdomen when it is about ready to be dropped.

Each species produces its own type of ootheca (Fig. 66). The oothecae are dropped at convenient places, and the eggs normally hatch in a month or two. The female may carry the egg case till the eggs are ready to hatch as in the case of the German roach (*Blatella germanica*).

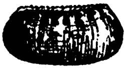

Fig. 66. Egg case of *Blatta orientalis.*

The four common, more or less domesticated species (Fig. 67) are *Blatella germanica* (the German roach or croton bug), *Blatta orientalis* Linn. (the oriental roach), *Periplaneta americana* Linn. (the American roach), and *Periplaneta australasiae* Fabr. (the Australian roach). Another species, the brown-banded roach (*Supella supellectilium* Serv.), has become established in the southern United States and to some extent in the North. These species may be recognized by the aid of the following key (adults):

1. Tegmina in male not reaching the end of the abdomen, covering only about two-thirds of it; in female tegmina represented by small pads. Length about 1 inch. Almost black without any markings (Fig. 67) .. .. *Blatta orientalis*
   Tegmina in both males and females reaching or extending beyond the end of abdomen; if not covering the abdomen then marked with two light bands, one at base of wings and another about one-third of length from base 2
2. Length of insect rarely more than ½ inch 3
   Length more than 1 inch 4
3. Color uniformly pale brown with two parallel dark stripes on pronotum (Fig. 67) .... *Blatella germanica*
   Color uniformly dark brown with two pale bands near the base of tegmina, one at base and another a third of the length from the base .... *Supella supellectilium*
4. Thorax yellow with two large blotches of chestnut brown; tegmina lacking a yellow submarginal stripe along basal third. Length from 1½ to 2 inches (Fig. 67) .... *Periplaneta americana*
   Thorax yellow, with base and one or two central spots black; tegmina with a pale-yellow, submarginal stripe along basal third. Length about 1 inch .... *Periplaneta australasiae*

The German roach or croton bug (*Blatella germanica*) is the smallest household roach. It is world-wide in distribution and the commonest species in

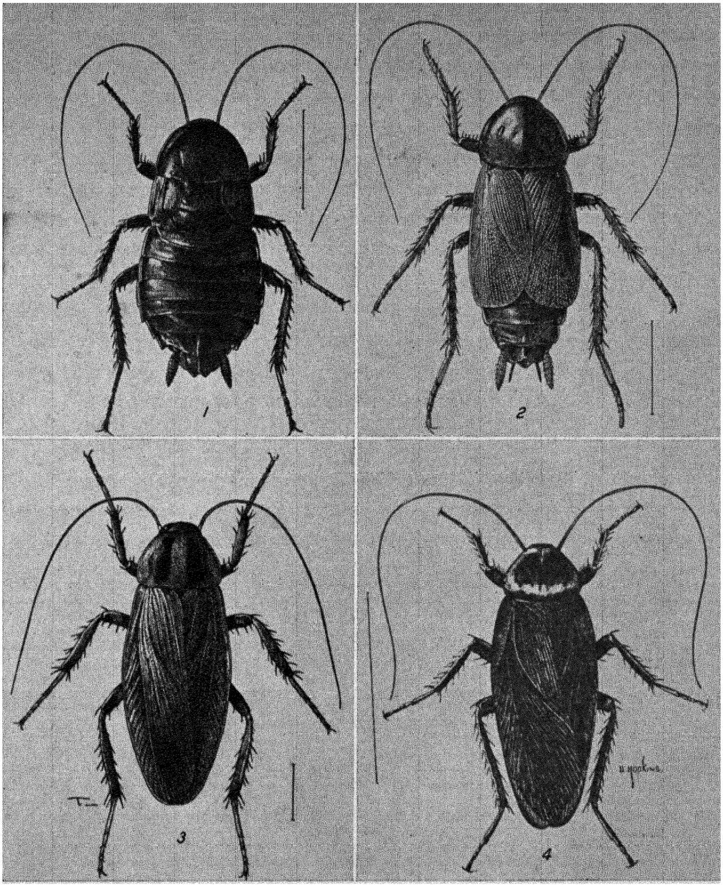

Fig. 67. Cockroaches. (*1*) *Blatta orientalis* (female). (*2*) *Blatta orientalis* (male). (*3*) ***Blattella germanica*** (female). (*4*) ***Preiplaneta americana*** (male). (From British Museum, after Laing.)

homes, restaurants, hotels, and similar places. The developmental period from the hatching of the eggs to the adult stage is from three to four months; the adults live from six to ten months. The American roach (***Periplaneta americana***) requires nearly a year to complete its developmental cycle though this varies greatly. The adults live a year or more. This roach is common on board ships and in warehouses, sugar refineries, meat-packing establishments, zoological gardens, city dumps, and similar places. In America it commonly invades our homes. Gould and Deay (1940) describe migrations of this species from place to place in the North. In the South along the Gulf coast it is common in palm trees, and nightly flights take place. It is known to be able to make long flights. The oriental roach (*Blatta orientalis*) is almost jet black in color and is primarily a house pest, preferring dark, warm basements, kitchens, and similar places. If food and favorable conditions of warmth and moisture are available, the developmental cycle from egg to adult requires nearly a year. The Australian roach (*Periplaneta australasiae*) is somewhat smaller than the American roach and is easily recognized by the pale-yellow streak on the tegmina. It is said not to be common in houses but prefers greenhouses and such places.

In addition, many other roaches occur in tropical and subtropical regions, and some of these may be distributed by commerce and adapt themselves to our homes and warm buildings. In recent years the brown-banded roach (*Supella supellectilium* Serv.) has spread into many parts of the United States and has become a house pest, especially in cities. It occurs as far north as Massachusetts, Wisconsin, South Dakota, and central California. Unlike other roaches this gregarious species prefers cupboards, shelves in closets, behind pictures and moldings, desks, and such places.

COCKROACHES AND HUMAN DISEASE: On account of their omnivorous and filthy habits and close association with man, cockroaches have long been suspected of disseminating pathogenic organisms. As they feed on man's food and his fecal wastes, roam at will through his household, and invade food shops, bakeries, meat-packing and food-storage plants, and similar places, it would be surprising if they did not distribute all kinds of organisms that are capable of surviving passage through their intestines or carriage on their bodies. Although various authorities have shown that viable bacteria can pass through the intestines of roaches and be carried on their bodies, yet nothing has been established of the importance of roaches in disease dissemination. Barber (1914) demonstrated that viable organisms of cholera pass through the intestines, but there are many other methods of dissemination of much greater significance. This is true also of such diseases as tuberculosis, typhoid, leprosy, and dysenteries, the etiological agents of which can survive passage through their intestines and be carried on their bodies. Such protozoan cysts as those of *Endamoeba histolytica, Endamoeba coli,* and *Giardia intestinalis,* survive and this may be of some significance. Investigations in Peru demonstrated that 7 per cent of the house-infecting cockroaches were carriers of viable cysts of *Endamoeba histolytica* (Schneider and Schields). As intermediate hosts of helminths they are of considerable importance. All four common cockroaches serve as intermediate hosts of the roundworms, *Gonglyonema pulchrum* (which is reported from rats and man), *G. neoplasticum* (which produces a carcinoma in the stomach of rats; not reported from man), *G. orientale* (a parasite of rats), and the acanthocephalid, *Moniliformis moniliformis* (a parasite of rats and occasionally of man).

CONTROL OF COCKROACHES: As roaches are lovers of filth and prefer darkened corners, cracks, and out-of-the-way places, the first procedure is a thorough clean-up and the destruction of all wastes. When this has been done, an application of sodium fluoride is one of the most effective methods of control. Commercial sodium fluoride, either pure or diluted with a carrier such as ground gypsum, chalk, or other diluent to give 50 per cent sodium fluoride, dusted or blown into all cracks, crevices, and runways and about sinks, tables, shelves, or other hiding places will quickly kill roaches. As the roaches run over the powder, it sticks to their bodies and in cleaning themselves they ingest the material, which proves a prompt poison. Of course, sodium fluoride should not be used near food or where there is a possibility of contaminating food. One treatment should be allowed to remain for several days, and the application is best made during the evening hours. The exposed dust should be cleaned up, but all in the cracks, crevices, and similar places should be allowed to remain since the powder remains effective almost indefinitely. This treatment should be repeated if all roaches are not destroyed by the first application.

Phosphorous pastes are purchasable and are quite effective. Smear the paste inside cardboard rolls and place them in the runways of the roaches. The pastes are particularly valuable in very damp climates because powders may harden and not be effective.

DDT as a powder or as a spray is very effective if properly and thoroughly applied. The dust should contain from 10 to 20 per cent of DDT, and all cracks, crevices, areas behind objects, baseboards, and runways should be liberally covered with the mixture. The visible dust may be removed in a few days but not that from the cracks and crevices. The application should be repeated in about five or six weeks to kill any young that may have hatched from eggs. A 5 per cent DDT oil spray is also effective but usually slower in action. Spray thoroughly and heavily with 5 per cent DDT in refined kerosene oil or as a 5 per cent emulsion. Carefully apply to all cracks, crevices, under draining boards, about sinks, on all runways, behind baseboards, and in similar places. Avoid contaminating food. The residual effect of the DDT will act for a considerable time.

Probably the most effective insecticide for the control of cockroaches is the recently developed commercial product known as chlordane. This material can be obtained from dealers, and full directions for its use will be found on the containers. Normally a 2 per cent solution is most effective. A combination spray containing 5 per cent DDT and 2 per cent chlordane is now on the market and is used as directed by the manufacturers.

THE ORDER HEMIPTERA: SUBORDER HETEROPTERA

The True Bugs

The order Hemiptera consists of two suborders, the Heteroptera and Homoptera. The Homoptera contain no insects known to be of medical importance. They are all primarily vegetarians sucking the sap from plants of all kinds. The Heteroptera are also mainly vegetarians, but a few families are predaceous, sucking the blood of other insects or attacking animals including man. Their chief characteristics are the possession of two pairs of wings (except the wingless forms): the fore wings are thickened at their bases (Fig. 68), and the membranous extremities overlap on the back; the hind wings are thin with few veins. The mouth parts consist of a jointed beak (Fig. 46) which contains the piercing and sucking organs; the beak arises from the front part of the head. The metamorphosis is gradual.

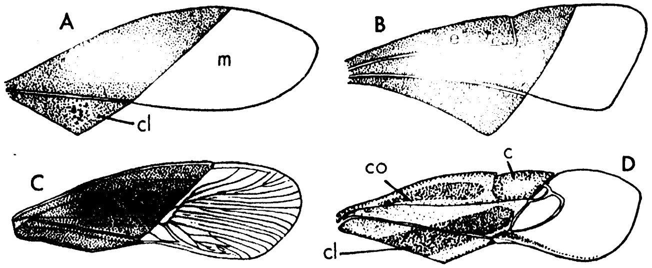

Fig. 68. Some hemelytra of the Heteroptera. (*A*) Diagrammatic illustration of hemelytra with the areas labeled. (*B*) Hemelytron of an *Anthocoridae* (*Triphleps*). (*C*) Hemelytron of a *Coreidae* (*Leptocoris*). (*D*) Hemelytron of a *Miridae* (*Poecilocapsus*). c, cuneus; cl, clavus; co, corium; e, embolium; m, membrane. (Modified from Comstock.)

The true bugs are abundant in species and individuals. Many species are very injurious to plants on account of their habit of piercing and sucking the sap; some are beneficial as they feed on noxious insects. Only two families contain species that are known to be injurious to man as bloodsuckers and as carriers and intermediate hosts of pathogenic organisms. Other families have certain species that may occasionally attack man and a list of these is given at the end of this chapter. The following brief key will aid in recognizing the principal families that may be noxious to man:

KEY TO THE FAMILIES OF THE HETEROPTERA RECORDED AS BITING MAN

1. Antennae shorter than the head and concealed in depressions on the underside of the head beneath the eyes. All forms aquatic 2
Antennae as long as or longer than the head and fully exposed 3
2. Hind tarsi consisting of two segments, the last bearing two distinct claws; large flattened bugs. Fore wing with the membranous portion with distinct veins. (The giant water bugs; Fig. 75) .... *Belostomatidae*
Hind tarsi consisting of three segments, the first very short and indistinct; tarsal claws setiform; head deeply inserted into prothorax. (Boat-shaped bugs, the back swimmers) .... *Notonectidae*
3. Beak composed of three segments 4
Beak composed of four segments 6
4. Beak stout, lying in a cross-striated groove but not reaching the middle coxae; ocelli, when present, placed distinctly behind the eyes or behind a transverse depression. (The assassin bugs) .... *Reduviidae*
Beak elongate, extending to middle coxae and groove not cross-striated; ocelli, when present, not placed as above 5
5. Ocelli absent; fore wings reduced, without membrane or vestigial. (The bedbugs) .... *Cimicidae*
Ocelli present; fore wings usually well developed; embolium present (Fig. 68). Membrane of fore wings veinless or with indistinct veins. (Flower bugs) .... *Anthocoridae*
6. Front legs fitted for seizing prey; fore tibiae and usually the front femora armed with stout spines which interlock .... *Nabidae*
Front legs fitted for walking, normal 7
7. Front wing with a V-shaped portion (cuneus) at the apex of the harde d base of the wing (Fig. 68); membrane with one or two closed
s. (Leaf bugs) .... *Miridae*
wings not as described above 8
absent. (Cotton stainers) .... *Pyrochorridae*
present; no transverse depression in front of the ocelli 9
rane of fore wing with five simple veins arising from its base.
nch bugs) .... *Lygaeidae*
ane of fore wing with many, usually anastomosing, veins arising
transverse basal vein. (Squash bugs) .... *Coreidae*

THE FAMILY CIMICIDAE—THE BEDBUGS

This is the well-known bedbug family. The most distinctive features are the depressed bodies, fitting them for creeping into cracks and crevices; the absence of wings except for the small padlike elytra (remnants of the fore wings, Fig. 69); the beak is segmented and lies in a groove on the ventral surface of the head and thorax; the head is short and broad and bears a pair of prominent compound eyes; the ocelli are absent; the antennae are four segmented.

The family contains three principal genera, *Cimex, Oeciacus,* and *Haematosiphon.* (Some five or six others have been described.) The entire family contains not over 35 well-defined species.

THE GENUS *CIMEX:* Several species have been described as belonging to this genus. Only two of them are consistent parasites of man. The common bedbug, *Cimex lectularius* Linn., and the tropical bedbug, *Cimex hemipterus* Fabr., are persistent invaders of human habitations and live primarily on human blood, though they readily feed on rabbits, mice, white rats, and fowls.

Cimex lectularius Linn. (the bedbug, wall louse, mahogany flat, etc.) is the common bedbug (Fig. 69) of the temperate zones. Its body is flattened dorsoventrally and is well adapted to its mode of life. The adult measures 4 to 5 mm. in length and about 3 mm. in width. It is reddish brown in color. The head is broad and flat and fits rather neatly into the deeply concave anterior part of the prothorax. The antennae are four-segmented; the last two segments are elongate and much thinner than the preceding. The eyes are prominent and deeply pigmented. The beak is three-segmented and lies in a groove reaching the middle coxae. The mouth parts are fully explained on pages 130–133. The thorax appears as a single segment, the large anterior part being the prothorax. Dorsally the mesothorax may be distinguished by the attachment of the reduced fore wings. The metathorax lies beneath and behind the fore wings. The abdomen consists of eight visible segments; the terminal ones (the ninth and tenth) are modified for sexual purposes (Fig. 70).

A great many insects possess a distinctive odor, and this is especi true of bedbugs, the "bedbuggy" odor of infested dwellings being very ed and easily recognized by anyone familiar with it. The odor of the produced by special stink glands, which, in the nymphs, open on t surface of the abdomen and on the ventral side of the last thoraci t of the adult. Puri has described these glands in great detail; he cons r function to be defensive and sexual.

The males and females of bedbugs can be recognized easily. Ir le

(Fig. 70) the abdomen gradually narrows from the third segment to the rather pointed tip, where are located the genitalia. In the female the abdomen does not narrow so much, and the tip is broadly rounded (Fig. 70). The external genital organ of the male consists of a sclerotized, sharply pointed aedeagus, which arises from the interior of the ninth segment. It is directed to the left side (seen from the dorsal surface). When not extended it lies in a groove of the segment. The aedeagus is grooved on its inner face, and at its base lies the penis. The anal opening is in front of the tenth segment, which appears to surround it. In the female the external genital organs consist of the genital opening surrounded and supported by sclerotized plates or gonapophyses. On the ventral surface of the abdomen of the female there is a rather sharp and deep depression or slit on the posterior margin of the fourth[1] segment, about halfway between the median line and the margin. This leads to a peculiar organ known as the organ of Berlese. It is through this organ that the male fertilizes the female, the sperm being introduced into it and not into the genital opening at the time of copulation. In mating the male

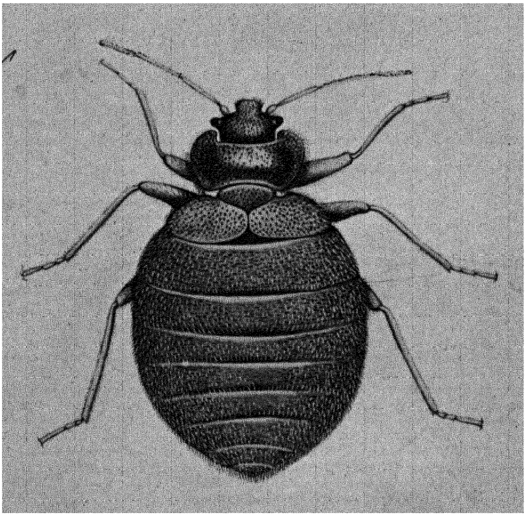

Fig. 69. The bedbug, *Cimex lectularius.* Female. (Courtesy Department of Agriculture, Division of Entomology, Canada.)

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[1] In reality the fifth segment as the first visible abdominal segment is the second.

inserts the aedeagus into the slit, the penis passes down the groove and ejects the sperm into the opening of the organ of Berlese.

BIONOMICS: Bedbugs are primarily parasites of man, though they feed on fowls, mice, and white rats and are frequently serious pests of rabbits in rabbitries. They are nocturnal in their feeding habits and during the day hide in convenient cracks, crevices, or other hiding places in sleeping rooms; under loosened wallpaper and moldings; in cracks in the flooring, old wooden bedsteads, and the creases and folds of mattresses; under bedding; and in places where mice, white rats, or rabbits are reared. As they are gregarious,

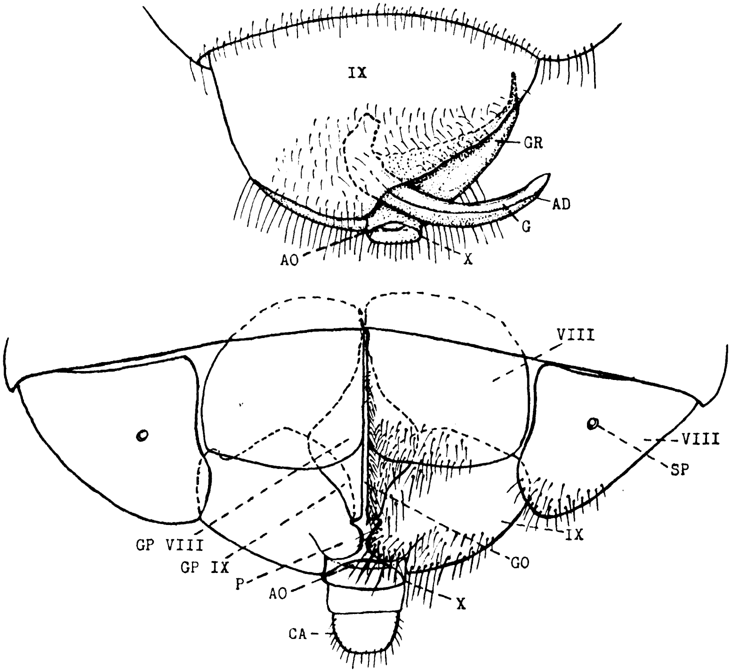
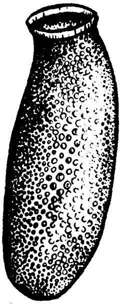


Fig. 70. Cimex lectularius. Upper: Tip of abdomen of male (ventral view). *Lower:* Tip of the abdomen of female (ventral view). AD, aedeagus; AO, anal opening; CA, cauda; G, groove in aedeagus along which penis moves in act of copulation; GO, genital opening guarded by two pairs of gonopophyses; GP VIII and GP IX, gonopophyses of the eighth and ninth segments; GR, groove in the ninth segment for the reception of the aedeagus; P, hairy process of the ninth segment; SP, spiracle; VIII, IX, X, eighth, ninth, and tenth segments.

large numbers may be found in infested rooms. Mating takes place at irregular intervals, and the eggs are laid in the hiding places of the bugs. The egg (Fig. 71) when laid is pearly white, gradually changing to a yellowish white. It measures 1.02 mm. in length by 0.44 mm. in width. The shell is distinctly reticulated and has a cap or lid that is pushed off when the nymph emerges. Each female is capable of laying from 75 to 200 eggs. Titschack records a single female that laid 541 eggs. The eggs are not all laid at one time but usually in ones, twos, threes, or small batches each day. Cragg records that a caged female, when supplied with food and its mate, laid 174 eggs in 105 days and only ceased laying at the approach of cold weather. The adults live a long time, at least six or seven months to a year. They can also withstand long periods of starvation, especially during cold weather when they become inactive. Adults have been kept alive without food for a year, and the nymphs can withstand varying periods of starvation, 70 days or more.



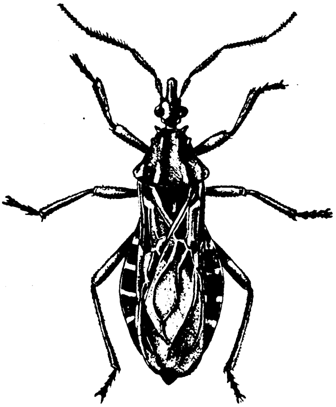


Fig. 71 (*left*). The egg of the bedbug, *Cimex lectularius.*

Fig. 72 (*right*). A large reduviid bug from South America, *Pangstrongylus* (*Triatoma*) *megistus.*

LIFE HISTORY: The egg hatches in from six to seven days (longer if the temperature is low). The first-stage nymph is very active and closely resembles the adult except in size. It will feed rather promptly. After feeding, the nymph hides in some convenient place to digest its blood meal and prepares to molt to the second instar. There are five molts, and the nymph takes, practically always, only a single blood meal between molts. According to Jones, the development period from egg to adult is a little over 30 days (the experiments were carried out at a temperature of 27° C. and a relative humidity of 75 per cent; the nymphs were fed to repletion between each molt). He found the length of the instars to be: first instar, 5 days; second, 4.5 days; third, 4.2 days; fourth, 4.6 days; and the fifth, 6 days. The nymphal life may be greatly prolonged by low temperatures, lack of food, or other factors affecting development. Both the nymphs and adults feed rapidly, repletion being reached in 5 to 10 minutes. Jones has shown the amount of blood required from the first instar to adult is only 0.0156 grams for the males and and 0.0209 grams for the females. The number of generations per year varies greatly, being largely dependent on food supply, temperature, and humidity. During the winter season the bedbug is usually inactive but will feed and breed under favorable conditions. In warm climates it probably breeds throughout the year, and the number of generations is probably five or six or more. In colder climates there are said to be three or four generations, but no definite number can be given as the reproductive and developmental rates are so dependent on food supply and warmth.

DISTRIBUTION: This bedbug is cosmopolitan, being found throughout the temperate regions of the world and probably in many tropical areas, though another species, *Cimex hemipterus,* is the abundant tropical bedbug.

Cimex hemipterus (Fabr.) is the so-called "tropical bedbug" and is widely distributed throughout the tropical and subtropical regions, especially Asia. It closely resembles the ordinary bedbug but can be distinguished by the lateral margins of the prothorax being rounded and the concave depression for the reception of the head being shallower. The habits of the nymphs and adults are very similar to those of the common bedbug. The life history is almost identical. Dunn found that the time from the hatching of the egg to the adult varied from 30 to 40 days. The most interesting feature was that each nymphal stage required from two to four meals instead of one. The adults live from six to eight months. Each female is capable of laying from about 100 to 439 eggs.

DISPERSAL: Bedbugs are gregarious and remain close to their food supply; their dispersal is mainly through man's activities. As bedbugs readily hide in clothing and the eggs are laid in all their places of concealment, their distribution is largely dependent on man's carrying them from place to place with his household goods or his clothing. A single impregnated female accidentally introduced into a household will soon produce a good-sized colony. Furthermore, bedbugs are active migrants and will readily pass from one person to another. This has been seen again and again in crowded railway cars, boats, buses, and other public conveyances. In crowded city houses, apartments, and tenements they will travel along the water and heating pipes, especially if their food supply has been removed. Bedbugs are frequently reported as very abundant in movie houses. Again bedbugs are capable of withstanding long periods of starvation, especially during cold weather, and unfrequented houses, as summer hotels, cottages, and similar places may remain infested from year to year. As they are known to feed on birds, white rats, rabbits, and mice (Patton and Evans record that they fed them on rats, cats, dogs, monkeys, rabbits, guinea pigs, and a calf), they can probably obtain food to tide them over periods of man's absence. MacGregor mentions an interesting case of dispersal. In the East African campaign of World War I bedbugs invaded the cork lining of the helmets of the soldiers. As the helmets were piled together at night, all soon became infested and the soldiers complained of bugs attacking their heads.

BEDBUGS AND HUMAN WELFARE: Bedbugs affect man in two ways: (1) by their bites and bloodsucking propensities; (2) by the possibility of their carrying disease-producing organisms or acting as hosts of parasites in some phase of the latter's developmental cycle.

BITES: Many persons suffer severely from the bites of bedbugs; many do not suffer at all or even know when they are bitten; and others appear immune to their attacks. Puri (1924) has shown that the salivary secretion is the cause of the irritation and that it contains a rather strong anticoagulin. Children suffer most from bedbug bites. In susceptible persons there is severe irritation, hardened wheals may develop at the sites of the bites, and secondary infection may follow. In severe cases there may be a marked nervous reaction accompanied by digestive disorders. Stiles records a case diagnosed as neurasthenia and treated as such; an examination of the patient's room showed an abundance of bedbugs; after fumigation a pint of bedbugs was collected and the patient promptly recovered. Unfortunately there is very little data on the effect of continued attacks of bedbugs. When abundant they cause loss of sleep, loss of blood, nervous reactions, digestive disturbances and, in general, reduce the vitality so that people, especially children, are more susceptible to prevalent diseases.

BEDBUGS AND DISEASE: Owing to the close relation of man and bedbugs it has long been thought such bloodthirsty parasites must, in some way, be associated with disease transmission. Though intensive research has been carried out along this line, nearly all the results are either negative or inconclusive. Bedbugs have been shown experimentally capable of transmitting bubonic plague (*Pasteurella pestis*) even as long as 48 days after an infective meal, yet there is no evidence that they play a part in human transmission. Many experiments with pathogenic organisms such as those of leprosy, tuberculosis, and typhoid fevers have given negative results. Extensive experiments with bedbugs and the causative agents of kala azar (*Leishmania donovani*) and of Oriental sore (*Leishmania tropica*) have resulted in failure to transmit even under the most favorable conditions. In the case of relapsing fevers (*Spirochaeta* spp.) all experiments have failed, though the bedbugs can be infected and the spirochetes remain alive in the gut or the coelomic fluid for considerable periods. No transmission took place by the bites of infected bedbugs though transmission of the spirochetes was effected by crushing infected bedbugs on the scarified skin of experimental animals or by injecting the hemolymph of such bedbugs. When relapsing fevers become epidemic in the presence of numerous bedbugs, human infection may occur, though usually the ordinary human lice (*Pediculus humanus*) are present and are effective transmitters. Brumpt has shown that the bedbug (both species) can be infected with *Trypanosoma cruzi* (causative agent of Chagas' disease), and he caused animal infection through the feces. This work was confirmed by Mayer and da Rocha-Lima. No infection occurred by the bites of infected bedbugs. Francis has shown that *Cimex lectularius* can transmit tularemia (*Bacterium tularense*) from mouse to mouse by its bites up to 71 days after the bugs had their infective meal. Mice also contracted the disease by eating bedbugs that had been infected 65 to 100 days previously. He also showed that the feces of infected bugs contained the virulent organisms of tularemia at all times to at least 250 days after the date of infection.

OTHER SPECIES OF CIMICIDAE: *Leptocimex boueti* (Brumpt) occurs in French West Africa and is quite widely distributed. According to Joyeux (1913) its life history is very similar to that of the ordinary bedbug as it readily feeds on man. It may be recognized by its very long legs and much narrower body. *Cimex pilosellus* Horvath and *C. pipistrelli* (Jenyns) are common parasites of bats, the former in America and the latter in Europe. These bugs will invade sleeping rooms and attack man when their normal hosts are driven away. In the genus *Oeciacus* the body is clothed with long hairs and the last two segments of the antennae are but slightly thinner than the preceding ones, and about equal in length; the front margin of the pronotum is shallowly concave. *O. vicarius* Horvath, the common bedbug of swallows in North America, will invade dwellings when their nests are located on houses and infested with this bug; *O. hirundinis* (Jenyns), the barn-swallow bug of Europe, will also attack man and its bite is said to be severe. *Cimexopsis* *nyctalis* List has been recorded in Nebraska as attacking man, though its normal hosts are thought to be chimney swifts (*Chaetura*). *Haematosiphon inodora* (Dugès) is a large bug that normally infests poultry houses in the southwestern United States and Mexico; it has also been reported from Florida. It sometimes invades houses and frequently becomes a serious pest. Its bite is severe.

CONTROL OF BEDBUGS: During World War II an almost perfect method for the control of bedbugs was developed. By the proper use of DDT bedbugs can not only be controlled but eliminated from all their breeding places. Depending on the place to be treated either a 5 per cent DDT solution or emulsion can be used. Where it is not feasible to use a spray, a 10 per cent dust may be employed, though it does not give such satisfactory results.

The 5 per cent DDT spray (solution or emulsion) can be applied by a small hand sprayer, by a knapsack type sprayer, or by power equipment. In treating an infested room or building it is essential first to clean the place. Then spray all beds, especially the mattresses, bedsprings, joints, and corners, thoroughly with a wet spray, not a mist. Then treat all cracks, crevices, especially behind baseboards, picture frames, loose wallpaper, and, if the place is badly infested, every part of the room. The spray will kill all bedbugs it covers, but many may not be reached. However, the residual DDT on the walls, bedding, and beds will kill all bugs that come in contact with it. Experiments have shown that the residual action is very lasting, at least a year. If spraying cannot be used, dust with a 10 per cent DDT powder on mattresses, bedding, cracks, crevices, and similar places. The bedbugs will be killed by walking over the powder. By the proper and timely application of any of these methods bedbugs can be eliminated.

Sulphur fumigation is also effective but it involves much more labor and trouble. When sulphur is used, the rooms must be prepared by the closure of all cracks, crevices (as around doors and windows), keyholes, and other openings by pasting over them strips of heavy brown paper. (Thin flour paste or merely water will serve for temporary attachment; soak the brown paper in water till saturated; then apply it and it will stick for several hours.) All metallic objects and fabrics that might be bleached by the sulphur fumes should be removed. Metals that cannot be removed should be coated with vaseline. Large openings such as fireplaces must be closed. The sulphur is used at the rate of four pounds to 1000 cubic feet of space. The sulphur should be burned in a large iron pan or pot placed on bricks in a galvanized tub containing some water. This will take care of any spilling and prevent injury to the floors. Pour a small amount of denatured alcohol on the sulphur (abou a cup to four pounds of the sulphur) and ignite the alcohol. Several such outfits may be placed in different parts of the place to be fumigated. All should be started at about the same time. Then the building should remain closed for several hours, at least four or five. Sulphur candles may also be used, but great care should be employed to avoid danger from fire and enough candles must be burned.

Fumigation with hydrocyanic acid gas is a very effective control method but should be undertaken only by responsible personnel. The building to be fumigated should be prepared as for sulphur fumigation. The necessary ingredients are sodium or potassium cyanide (these can be obtained in the form of small eggs, each weighing about one ounce), a commercial grade of sulphuric acid, and water. It requires at least one ounce of the cyanide for each 100 cubic feet of space. The mixture is prepared as follows:

Sodium cyanide (95 to 97 per cent purity)	1 ounce
Sulphuric acid	1½ fluid ounces
Water	2 fluid ounces

In the fumigation of a building, the cubic contents must be calculated, the distribution of the fumigation pots should be designated, and the amount of ingredients for each pot determined. The equipment should consist of five- to eight-gallon earthenware crocks. The crocks should be placed on thick folds of paper to avoid injury from splashing. In each of the crocks place the determined amount of water and then add the sulphuric acid, pouring slowly (*never* the reverse process). Beside each crock place the determined amount of sodium cyanide, preferably in a thin paper bag. When all is in readiness start at the top floor and drop the cyanide into the jars, passing to the floors below as rapidly as possible. The gas is very light and is given off very rapidly. The house or building should be kept closed for at least 12 hours and then aired by opening the windows and doors from the outside. Keep open for another 6 to 12 hours before entering unless gas masks are used. Fumigation with hydrocyanic acid gas should be undertaken only by trained persons and gas masks should be used.

Another fumigation method is the use of thin discs impregnated with liquid hydrocyanic acid. These discs (Zyklon discoids) are conveniently packed, and full directions for their use are furnished. Gas masks should be employed when using such discs. Pyrethrum aerosol bombs are also effective and they are nonpoisonous.

In most of our states and particularly our large cities the Boards of Health have strict regulations governing the use of poisonous gases. Such rules and regulations should be carefully followed before attempting any fumigation.

THE FAMILY REDUVIIDAE—THE ASSASSIN BUGS

The Reduviidae is a large family of predaceous bugs that suck the blood and lymph of their prey. At least 4000 species are known. They feed mainly on other insects and on each other. However, certain groups attack man and some of these are important vectors of human and other animal diseases. Their bites are frequently severe and often difficult to heal. The assassin bugs are rather elongate, active, large insects. The beak is stout, three-segmented, and capable of inflicting a painful wound. The head is freely movable and more or less elongate, and the eyes are conspicuous. The ocelli are prominent when present and the antenna is four-segmented. The family is divided into a large number of subfamilies and numerous genera. Although nineteen subfamilies are listed by Usinger (1943), only about three contain genera that are at present known to plague man, and some of these are not of great importance. The following brief summary may aid in recognizing these subfamilies:

KEY TO THE SUBFAMILIES HAVING SPECIES THAT ATTACK MAN[2]

1. Beak divided into 3 segments and fits into a cross-striated groove; stout, short, not reaching the middle coxae; ocelli, when present, placed distinctly behind the eyes or behind a transverse depression .... Family *Reduviidae* 2
2. Wing membrane with one or more closed cells; front coxae not greatly elongated, usually less than twice as long as broad and not extending beyond apex of head 3
3. Pronotum constricted behind the middle; ocelli present. Subfamily *Piratinae* (Genera *Melanolestes, Rasahus,* and others; Fig. 74)

   Pronotum constricted at or near the middle 4
4. Ocelli present and located behind the compound eyes; second antennal segment not subdivided 5
5. Head rarely constricted behind the eyes. Elongate; ocelli located on oblique elevations or tubercles at posterolateral angles of the long, cylindrical head; dorsal abdominal glands absent .... Subfamily *Triatominae* (Here belong *Psammolestes, Rhodnius, Eratyrus, Panstrongylus, Triatoma,* and others)

   Head transversely constructed behind the eyes; eyes not stalked; antennae

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[2] Keys to the genera and species of Triatominae will be found by consulting the references at the end of the chapter.

not inserted on long, oblique tubercles; dorsal scent glands present ......
(*Reduvius, Spiniger,* and others) .... Subfamily *Reduviinae*

The Subfamily Triatominae

The known members of this subfamily as at present restricted feed exclusively by sucking the blood of vertebrates. Though widely distributed, the great majority of the species are predominantly American. A few species occur in the Oriental and African regions, and *Triatoma rubrofasciata* (De Geer) is tropicopolitan. Usinger (1944) recognizes 9 genera and 40 species and subspecies from North and Central America, Mexico, Panama, and the West Indies. Costa Lima (1940) recognizes 9 genera and 44 species from Brazil and neighboring countries. Neiva and Lent (1941) list 14 genera and 89 species from the world. The study of this subfamily is of great importance in the Americas since the discovery by Chagas (1909) that a certain species, *Panstrongylus megistus,* is the intermediate host of a disease (Chagas' disease) caused by *Trypanosoma cruzi.* Since then a large number of species have been shown to harbor the trypanosome and many of them to transmit the disease. Only a few of the species can be discussed here with a list of the more important vectors of the disease and their known distribution.

Panstrongylus megistus (Burm.) was the first species shown by Chagas to be the natural vector of the disease that bears his name. The species is widely distributed in Brazil, British Guiana, and Paraguay. This bug is primarily domestic and hides in cracks, crevices, or any available cover during the day. At night it comes out to feed and its bite is not recorded as severe. The adults measure from 30 to 32 mm. in length. They are black, with regularly arranged red markings on the prothorax, wings, and abdomen (Fig. 72). They are strong fliers and readily migrate from house to house. The female lays her eggs in batches (8 to 12 in a batch) in the cracks, crevices, and holes in the floors and walls. Each female lays from 160 to 220 or more eggs. The eggs hatch in from 8 to 30 days. The nymphs feed on humans at night. There are five nymphal stages and each nymphal stage requires a number of blood meals. The entire life cycle from egg to adult varies from 260 to 300 days.

Triatoma rubrofasciata (De Geer) is widely distributed in the Oriental regions, parts of the Ethiopian region, neotropical region, the West Indies, Central America, and Florida in the United States. It is quite domestic in its habits and its bite is rather severe. Its life history is very similar to that of the preceding species. Patton and Cragg found, under experimental conditions, that the life cycle from egg to adult required from four and one-half to five months.

Triatoma sanguisuga (Le Conte) is the big bedbug or conenose (Fig. 73) of the south and western United States, extending north to Pennsylvania and west to Kansas, Texas, and Mexico; it is reported from Panama. It infests poultry houses and the adults invade human habitations. The adult is 18 to 20 mm. in length, flattened, and dark brown in color with pinkish or reddish-orange areas on the abdomen, on the tips and bases of the hemelytra, and along the anterior and lateral margins of the pronotum. Recently several subspecies have been described but on rather minor characters.

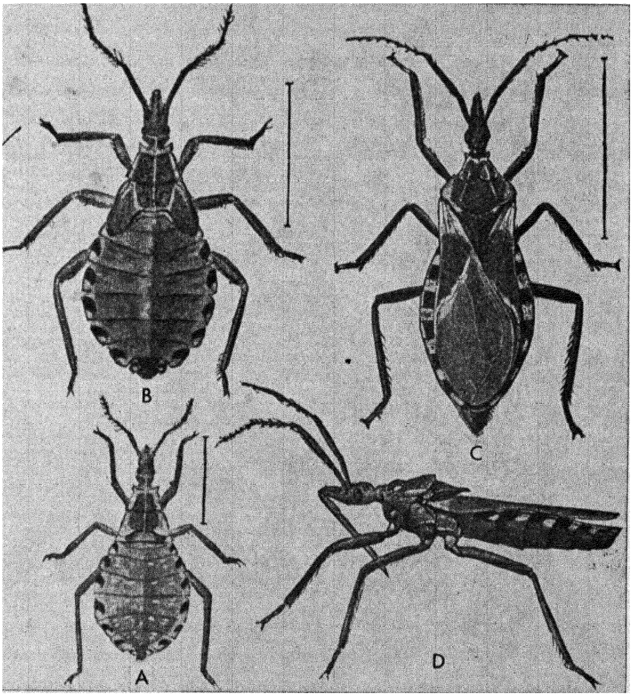

Fig. 73. The bloodsucking conenose, *Triatoma sanguisuga.* (*a*) and (*b*) Nymphal stages. (*c*) Adult. (*d*) Lateral view of adult to show long beak. (After Marlatt.)

The life histories of a number of species have been fully elucidated in recent years: *Euratyrus cuspidatus* Stål and *Panstrongylus geniculatus* (Latr.) by Hase (1932); *Rhodnius prolixus* Stål by Buxton (1930); *Triatoma dimidiata* (Latr.) by Campas (1923); and *Paratriatoma hirsuta* Barber (two-year life cycle), *T. rubida uhleri* (Neiva), one-year life-cycle, *T. lecticularius occulata* (Neiva), one-year life cycle, *T. gerstaeckeri* (Stål), one-year life cycle, *T. longipes* Barber (two-year life cycle), and *T. protracta* (Uhler), one-year life cycle, all by Usinger (1944).

TRIATOMINAE AND THEIR RELATION TO DISEASE: BITES: The bites by a number of species are known to be severe but others cause little if any reaction. Numerous records of severe reaction from their bites are known. However, Wood (1942) tested eight common species (*Triatoma protracta woodi, T. longipes, T. gerstaeckeri, T. lecticularius, T. sanguisuga, T. rubida,* and *Paratriatoma hirsuta*) without any ill effects except a tickling sensation.

DISEASE: The only disease so far definitely associated with these bugs is Chagas' disease caused by *Trypanosoma cruzi.* In 1909 Chagas announced successful transmission of an unknown disease in Brazil by *Panstrongylus megistus* caused by a trypanosome and described by him as *Trypanosoma cruzi.* This disease was later differentiated as a specific entity and bears the name of Chagas' disease. The disease is widespread and occurs from Argentina through much of South America, Panama, Central America, and Mexico. The disease is characterized by fever, swelling of the eyelids and face, enlargement of various lymphatic glands, and destruction of the cardiac muscles of the heart, the cells of the spleen and the brain, and endothelial tissue cells generally throughout the body. The disease appears in two forms, acute and chronic. In the acute stage death may occur in two to four weeks. In the chronic state, mostly in adults, the disease runs a varied course. At present there seems to be no adequate treatment.

TRANSMISSION: The various species (see Table 6) obtain the trypanosomes from the infected reservoir hosts when taking blood. In the bug the trypanosomes develop only in the lumen of the intestinal tract. First they develop into crithidial forms in the stomach; migrating posteriorly they transform to smaller forms and give rise to the metacylic (infective) trypanosomes. These are discharged in the feces, and infection in man takes place when the feces are deposited at the time the bug is feeding or soon after. They gain access to the body through abrasions of the skin (by scratching or otherwise) or the mucous membranes of the mouth, conjunctiva of the eyes, or other moist membranes. Other animals become infected in a similar manner or by eating infected bugs. The life cycle in the bug requires 6 to 15 days, and once infected the bug remains capable of transmitting the disease for a long time, at least one or two years according to some authorities. In man the incubation period is 10 to 12 days and the trypanosomes may be found in the blood during this period. Later they disappear from the blood and are found in the *Leishmania* form in the cardiac muscles and in cells of the spleen, liver, brain, and most of the tissues. From time to time the trypanosome form appears in the circulating blood and man may serve as a reservoir for the bugs. As this disease is widespread, it has become of great importance. Though the trypanosome is present in many triatome bugs in the United States, no human case has been discovered. However, these infected bugs do bite humans and Packchanian (1943) has produced a typical infection in a human being with trypanosomes from Texas (crushed infected *Triatoma heidemanni*). He also infected monkeys (*Macacus rhesus*) and deer mice (two species). He recovered the trypanosomes from all cases and cultured them. Despite this experimental evidence no human cases of Chagas' disease have been isolated in the United States. Undoubtedly some must occur, but they have not been diagnosed as such.

Table 6. Tritome bugs found naturally infected and their distribution.

Species	*Distribution*
1. *Triatoma barberi* Usinger	Mexico
2. *Triatoma brasiliensis* Neiva	Brazil
3. *Triatoma chagasi* Brumpt and Gomes	Brazil
4. *Triatoma delpontei* Romana and Abalos	Argentina
5. *Triatoma dimidiata* (Latr.)	Mexico, Central America, Panama, Venezuela, Peru
6. *Triatoma gerstaeckeri* (Stål)	Mexico, U.S.A.
7. *Triatoma hegneri* Mazzotti	Mexico
8. *Triatoma infestans* (Klug.)	Brazil south to Argentina, Chile, Peru
9. *Triatoma lecticularius* (Stål) (*heidenmanni* Neiva)	U.S.A. (Texas)
10. *Triatoma longipes* Barber	U.S.A. (Arizona)
11. *Triatoma phyllosoma* (Burm.)	Mexico
var. *longipennis* (Usinger)	Mexico
var. *pallidipennis* (Stål)	Mexico
var. *picturata* (Usinger)	Mexico
12. *Triatoma platensis* Neiva	Argentina
13. *Triatoma protracta* (Uhler)	California, New Mexico, Arizona, Texas
var. *woodi* (Usinger)	Texas
14. *Triatoma rubida uhleri* (Neiva)	U.S.A. (California and Arizona)
15. *Triatoma rubrofasciata* (de Geer)	Tropical regions of world
16. *Triatoma rubrovaria* (Blanchard)	Argentina, Chile, Uruguay
17. *Triatoma sanguisuga* (Lec.)	U.S.A., Mexico, Panama
var. *ambigua* (Neiva)	U.S.A.
var. *indictiva* (Neiva)	U.S.A. (Arizona, New Mexico, Texas) and Mexico
18. *Triatoma spinolai* Porter	Chile
19. *Triatoma vitticeps* (Stål)	Brazil

20. *Dipetalogaster maximus* Usinger	Mexico (cape region of Baja California)
21. *Eutriatoma maculata* (Erichson)	Brazil north to Venezuela
22. *Eutriatoma nigromaculata* (Stål)	Venezuela
23. *Eutriatoma oswaldoi* (Neiva and Pinto)	Argentina
24. *Eutriatoma patagonica* del Ponte	Argentina
25. *Eratyrus cuspidatus* Stål	Panama, Colombia, Venezuela
26. *Neotriatoma circummaculata* (Stål)	Argentina, Uruguay
27. *Panstrongylus geniculatus* (Latr.)	Argentina north to Venezuela, Panama
28. *Panstrongylus megistus* (Burm.)	Paraguay, Brazil north to Venezuela
29. *Panstrongylus rufotuberculatus* (Champion)	Panama, Ecuador, Venezuela
30. *Rhodnius brumpti* Pinto	Brazil
31. *Rhodnius domesticus* Neiva and Pinto	Brazil
32. *Rhodnius pallescens* Stål	Panama
33. *Rhodnius prolixus* Stål	Brazil north to Colombia, San Salvador, Mexico
34. *Cavernicola pilosa* Barber	Brazil
35. *Psammolestes arthuri* (Pinto)	Venezuela

In addition to the list of species given above, a long series of other Hemiptera are recorded as capable of acting as vectors of Chagas' disease. Some of these are *Cimex lectularius, C. hemipterus, C. stadleri, Leptocimex boutei, Oeciacus hirundinis,* and *Haematosiphon inodora.* The following ticks are also indicated: *Ornithodoros moubata, O. talaje, O. venezuelensis* (*rudis*), *O. coniceps, O. lahorensis, O. nicollei, Amblyomma cajennense,* and *Rhipicephalus sanguineus.*

The vectors of Chagas' disease do not, in most cases, normally live in human dwellings but feed on a great variety of wild animals. Many of these animals serve as a reservoir for the trypanosome since none of the bugs are known to transmit *Trypanosoma cruzi* to their offspring. Furthermore many of the triatomes feed on more or less specific hosts, and a large number of these hosts have been examined and found to harbor *Trypanosoma cruzi* either in their blood or as *Leishmania* forms within tissue cells. From these hosts the triatome bugs obtain their infection and may transmit it to man. Some of the known reservoirs are: armadillos (8 or more species) in Brazil, Panama, Mexico, and Texas (mostly *Dasypus novemcinctus* and its varieties); bats in Panama and California (*Artibeus jamaicensis, Carollia perspicullata azteca, Desmodus rotundus murinus, Glossophaga soricina leachi, Phyllostomus hastatus panamensis,* and *Uroderma bilobatum* in Panama; *Antrozous pallidus pacificus* in California); cats and dogs in Brazil, Panama, Guatemala, and Mexico; house mice in the United States; opossums in Honduras, Panama, and the United

States; wood rats (*Neotoma* species) in Mexico, California, Texas, and other states. In addition, many animals are easily infected experimentally as mice (10 or more species), monkeys, rats, rabbits, dogs, and many others.

OTHER REDUVIID BUGS THAT SUCK BLOOD: A large number of reduviid bugs have been recorded as occasionally attacking man, and their bites frequently prove very annoying. The following are the most important species:

Rhodnius prolixus Stål is a domestic bug prevalent in parts of South America and San Salvador. It readily bites man and is the natural vector of Chagas' disease in Venezuela.

Reduvius personatus Linn. (Fig. 74) has received a rather bad reputation for attacking people and has been called the "kissing bug." This bug is commonly found in houses in many parts of the world. The nymphs are covered with a sticky substance to which dirt, dust, and floss adhere. They are said to feed on bedbugs, flies, etc., and the nymphs are frequently called the "masked bedbug hunters." The adult is almost coal black, very active, and attracted to lights. It measures about 20 mm. in length. When handled roughly as in attempts to remove them when they alight on the face or hands, they bite readily and fiercely. Herms quotes reporting physicians as stating, "In a few minutes after the bite the patient develops nausea, palpitation of the heart, rapid breathing, rapid pulse, followed by profuse urticaria all over the body." Like all other insect bites, the effects depend largely on the susceptibility of the individual.

Rasahus biguttatus Say (Fig. 74) and *Rasahus thoracicus* Stål are known as the "Corsairs." The former occurs in the southern states and the West Indies, the latter in the western part of the United States and probably Mexico. The bites of these bugs are quite severe and have been confused with spider bites.

Arilus cristatus Linn. the "wheel bug," so-called because of the cogwheellike crest on the prothorax, is normally predaceous on other insects. Hall (1924) records a young girl being bitten twice by this bug on her little finger. This was followed by severe pain, and growths resembling papillomas developed at the sites of the bites. The growths persisted for months, and the finger remained warmer than the others for over a year. The bug is distributed in North America from New Jersey southward.

Melanolestes picipes H. S. (Fig. 74) is an almost coal-black bug found commonly throughout North America. There are well-authenticated records of its biting man. It is found under stones, logs, moss, etc., and will bite if handled roughly. It is also reported as flying into houses, being attracted by the lights, and biting. Its bite is said to be severe.

Melanolestes abdominalis H.S. is also recorded as biting man. It is widely distributed in North America and has about the same habits as *M. picipes.*

Many other species of Hemiptera have been reported as occasionally attacking man. The reports of the effects of their bites vary so widely that no general statement regarding them can be made. It should be borne in mind that the bite of a bug is always more or less complicated not only by the susceptibility of the individual to protein substances (fluid from the salivary or poison glands of the bug) but also to any contamination present on the proboscis. The latter feature seems often to be overlooked when the ill effects of a bite are described. The following incomplete list will give some idea of the numerous observations recording the bloodsucking habits of bugs:

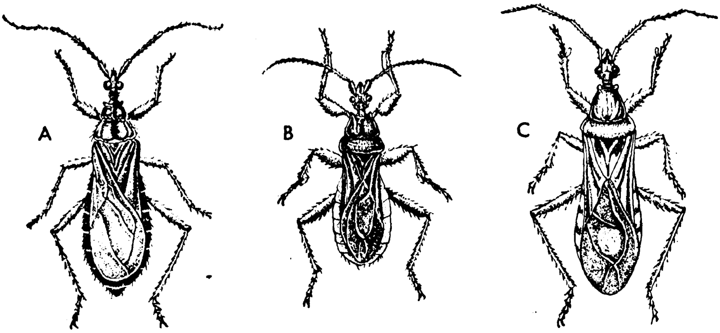

Fig. 74. Three reduviids that commonly bite man. (*A*) *Reduvius personatus* (the so-called "kissing bug"). (*B*) *Melanolestes picipes.* (*C*) *Rasahus biguttatus.*

Nabidae

Nabis capsiformis Germar. Cosmopolitan in the tropics.

Anthocoridae

Anthocoris musculus Say. Biting hop pickers.
Anthocoris sylvestris Linn. Europe.
Anthocoris kingi Brumpt. Sudan.
Anthocoris insidiosus Say. North America. Several records of this bug biting man.
Cardiastethus elegans Uhl. Panama. From bats.
Lyctocoris campestris Fabr. Europe and North America.

Pyrochorridae

Clerada apicicornis Sign. Widely distributed in the tropics.
Dysdercus superstitiosus Fabr. Africa.

Lygaeidae

Leptodemus minutus Jakovleff. Mediterranean region.
Geocoris heoni Puton and *G. scutellaris* Puton. North Africa.

Miridae (*Capsidae*)

Plagionathus obscurus Uhler. North America.
Lygus pratensis Linn. North America, Europe, Asia.

Notonectidae

These are aquatic insects, the so-called "back swimmers." Practically all the larger species will bite if handled roughly. The bite is quite severe.

Belostomatidae

These are the giant water bugs (Fig. 75) and include the largest of our Hemiptera; some species exceed three inches in length. They are found commonly in stagnant water. The adults are strongly attracted to lights and hence have been called "electric light bugs." Their bites, especially those of the larger species, are quite severe. The author has recorded the death of a good-sized woodpecker, killed by *Lethocerus americanus;* the bug had inserted its beak deep into the back part of the skull.

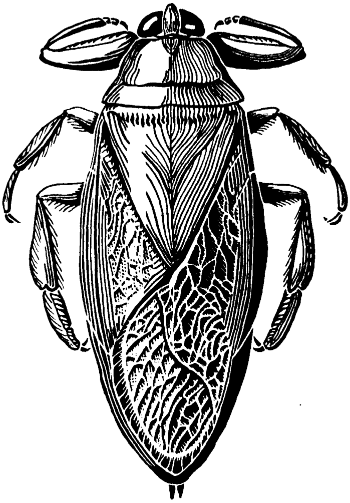

Fig. 75. A giant water bug, *Benacus griseus.*

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CHAPTER VII

The Order Anoplura: The Biting and Sucking Lice

THE order Anoplura contains the sucking lice and the biting lice of mammals and birds. It has been generally held, and still is by some, that these two groups constitute distinct orders, the Siphunculata (the sucking lice) and the Mallophaga (the biting lice). However, all the recent morphological and biological evidence seems to indicate that the two groups are so closely related that they constitute but suborders of the Anoplura.

CHARACTERISTICS

The Anoplura are wingless insects that live permanently as ectoparasites on mammals and birds, upon whose hairs (and clothes in man) or feathers they cement their eggs. The antennae are short, three- to five-jointed; the eyes are reduced or absent; the ocelli are lacking. The mouth parts are strikingly modified either for piercing and sucking blood (Siphunculata) or for feeding on the scales, feathers, scurf, and wastes of the skin (Mallophaga). The thoracic segments are more or less fused; the legs are rather short and fitted for clinging; the tarsi are one- or two-jointed and terminate in one or two claws. The metamorphosis is incomplete.

The order contains two suborders, the Siphunculata and the Mallophaga. The Mallophaga are not known to transmit disease.

THE SUBORDER SIPHUNCULATA

The Siphunculata or sucking lice are all permanent ectoparasites of mammals. The mouth parts (Fig. 79) are highly modified and, when at rest, are retracted within a diverticulum that opens into the floor of the pharynx at its anterior end. The thoracic segments are fused (except in the genus *Haema-*

tomyzus); the tarsi are one-segmented and terminate in a single claw which is fitted for grasping and clinging to hairs.

The Siphunculata is a very small group (only somewhat over 200 species have been described from the world), consisting exclusively of bloodsucking ectoparasites of mammals. At the present time four families are recognized.[1] Of these families only one, the Pediculidae, contains species that affect man himself. The following simple key will aid in distinguishing the families:

1. Head prolonged as a narrow tube; tibiae lacking a thumblike process opposing the claw; prothorax distinct. (Only one genus and one species, *Haematomyzus elephantis,* on elephants) .... *Haematomyzidae*
   Head not prolonged as a tube; tibiae with a thumblike process (Fig. 78) opposing the claw; prothorax not distinct 2
2. Body distinctly flattened; sparsely clothed with setae or spines that are arranged in more or less definite rows; parasites on land mammals 3
   Body rather thick and stout; clothed with stout, heavy spines, and, in some cases, scales. Parasites exclusively on marine mammals .... *Echinophtheriidae*
3. Eyes present, pigmented; head not retracted into the thorax. Parasites of man, monkeys, and apes .... *Pediculidae*
   Eyes absent or vestigial; head rather deeply retracted into the thorax. (This family contains more than half of the described species of lice) .... *Haematopinidae*

THE FAMILY PEDICULIDAE

The family Pediculidae[2] has been divided into two subfamilies, the Pediculinae and the Pedicininae. The former are characterized by a five-jointed antenna and occur on man, monkeys, and apes; the latter have the antenna three-jointed (indistinctly five-jointed) and are found on monkeys. The entire family contains some four genera and less than twenty species and varieties, many of them scarcely deserving the designation of more than races. The forms known from man are *Pediculus humanus* Linn., of which there are two varieties or races—*P. humanus* var. *capitis* de Geer (the head louse) and *P. humanus* var. *corporis* de Geer (the body louse)—and *Phthirus pubis* (Linn.) (the groin, crab, or pubic louse).

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[1] Ewing (1929) recognizes six families, but the creation of two new families for a few rather aberrant species does not seem warranted.

[2] Ewing (1929) has created a new family for the pubic louse (*Phthirus pubis* Leach); has accepted most of Fahrenholz's genera and species; and, at the same time, has described a number of new varieties.

THE HEAD LOUSE: *Pediculus humanus* var. *capitis* de Geer (Fig. 76) is the head louse of man. This variety or race is found principally on the head, living amongst the hair, on which it cements its eggs. It is found most commonly at the back of the head and above the ears, though the entire scalp may be infested. It also may occur on the eyebrows and the hairy parts of the body, and I have seen the eyelashes of an infant with a louse deeply embedded at the base of nearly every hair. On the average it is smaller than the body louse. The female measures about 2.4 to 3.3 mm. in length and the male averages about 2 mm. It is grayish in color, with the margins of the abdomen somewhat darker or almost black. In the male (Figs. 76,80) the abdomen is rounded at the posterior end and the male genital organ, the aedeagus, is easily visible and usually extruded; in the female the terminal portion of the abdomen is deeply cleft (Fig. 76).

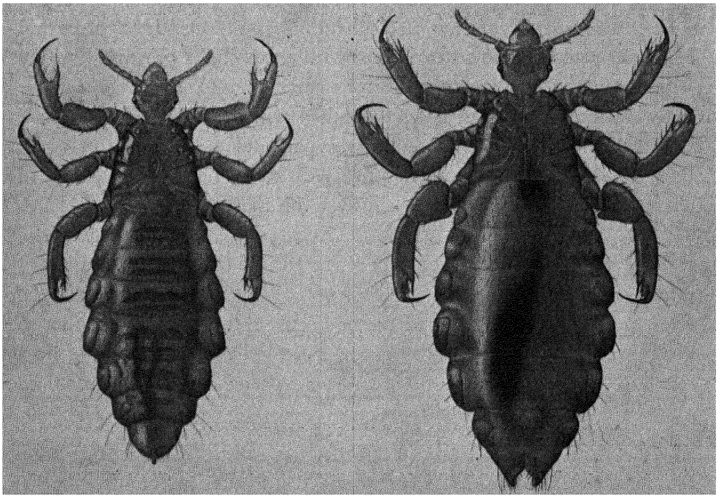
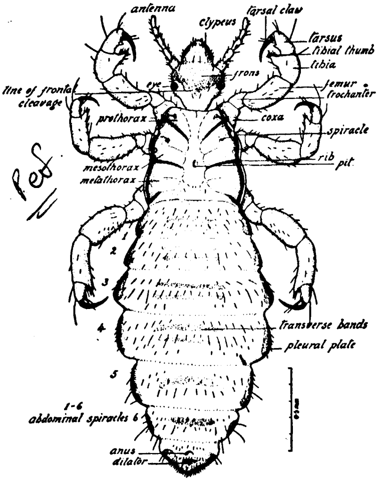


Fig. 76. The human louse, *Pediculus humanus.* Male at left, female at right. (After Nuttall.)

THE HEAD: In this louse the head is rounded in front and rather bluntly pointed; it is sharply constricted at the insertion of the antennae, then bulges sharply and gradually narrows to the neck. The neck is short but permits of considerable movement. The antennae are short and five-jointed. The eyes are prominent, heavily pigmented, but without facets. The thorax appears as a consolidated box widening posteriorly. To it are attached the legs, and there is a single pair of spiracles on the mesothoracic segment. The abdomen consists of nine segments, seven of which can be easily counted. The margins are festooned and chitinized to form darkly pigmented plates on which spiracles are located. There are six pairs of abdominal spiracles.

THE LEGS: This louse has stout legs, well fitted for clasping and holding. The coxa, trochanter, femur, and tibia are well developed (Fig. 77). The


antenna
tarsal claw
clypeus
tarsus
tibial thumb
tibia
frons
eye
femur
trochanter
line of frontal cleavage
prothorax
coxa
spiracle
rib
pit
mesothorax
metathorax
1
2
3
4
5
1-6 abdominal spiracles 6
transverse bands
pleural plate
anus
dilator

Ref

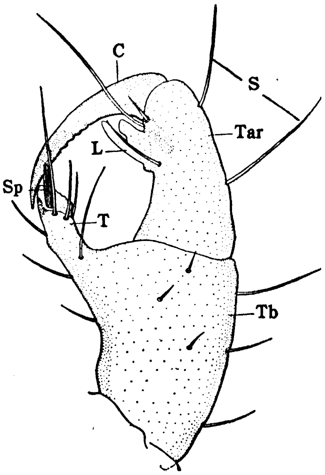

C
S
Tar
L
Sp
T
Tb

Fig. 77 (left). Pediculus humanus. Male with parts labeled. (After Nuttall, *Parasitology.*)

Fig. 78 (right). Pediculus humanus. Terminal portion of first left leg of male. C, claw; L, lamella; S, sensory spines; Sp, chitinous spine of thumb; T, tibial thumb; Tar, tarsus; Tb, tibia. (After Nuttall.)

tarsus consists of a single segment and bears a stout, recurved claw. The claw can be firmly apposed to a peculiar extension of the inner distal end of the tibia, the so-called "tibial thumb" (Fig. 78). The tibial thumb bears a prominent spine, and by apposing the claw against it the louse can attach very firmly to hairs. In the male the tibial thumb is better developed than in the female.

MOUTH PARTS: The mouth parts (Fig. 79) of lice are extremely complicated. They have been fully elucidated by Sikora (1916), Harrison (1916), Peacock (1918), and Florence (1921), but these workers are not entirely in agreement. At the front of the head is found a tubelike projection, the haustellum. It is

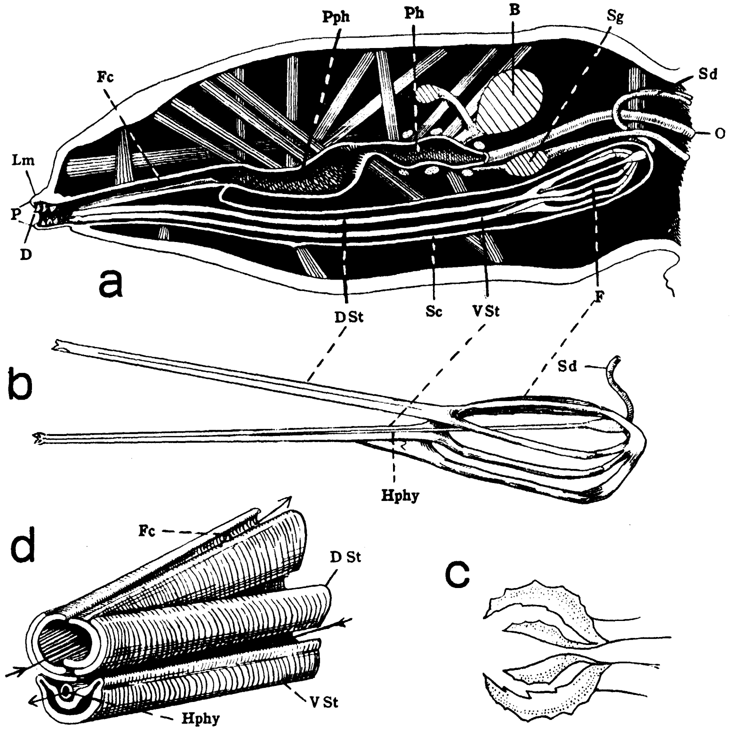


Fig. 79. The mouth parts of a louse (*Pediculus humanus*). (*a*) Longitudinal section of the head to show the relation of the various parts. (*b*) The stylets removed and shown more in detail. (*c*) The tip of the ventral stabber or stylet (greatly enlarged). (*d*) Reconstruction of the mouth parts near the anterior end to show passage of food canal between the dorsal stabbers or stylets. B, brain; D, denticles or teeth; DSt, dorsal stylet; F, forks of the stylets; Fc, food channel; Hphy, hypopharynx; Lm, labrum; O, esophagus; P, proboscis; Ph, pharynx; Pph, prepharynx; Sc, ventral sac holding the stylets; Sd, salivary duct; Sg, subesophageal ganglion; VSt, ventral stylet. In *d* the arrows indicate the direction of the passage of blood and salivary fluid. (Redrawn and modified after various authors.)

convex above and has an open slit on the ventral side. Within the haustellum are minute denticles (15–16), the buccal teeth. When the louse feeds, these denticles are everted and they serve as holdfasts or anchors while the main mouth parts are brought into play. The food channel extends from the haustellum to the pharynx. Ventral of the food channel and extending to the posterior end of the head is a long, narrow diverticulum, which opens anteriorly near the buccal plate. Within this diverticulum lie the piercing mouth parts. They consist of dorsal and ventral piercers or stabbers. The dorsal stabber is a single stylet; the ventral consists of two stylets closely appressed to each other. The piercers resemble long-handled, two-pronged forks, the prongs being posterior. Between the dorsal and ventral stabbers lies the salivary duct or pipe. All these structures are supplied with a complicated muscular system (Fig. 79).

METHOD OF FEEDING: When ready to feed, the louse applies its head to the skin. By muscular action the haustellum is everted and the teeth are anchored in the skin. The stabbers are brought forward, passing into the skin along with the salivary duct. Salivary secretion is poured into the wound (Nuttall, 1917, has shown that this secretion possesses an anticoagulin), and the pumping pharynx (Fig. 79) pumps the blood with great rapidity. The pumping action and the passage of the blood into the pharynx and thence to the esophagus and intestine can be seen most readily in freshly molted individuals.[3]

THE DIGESTIVE SYSTEM: The digestive system (Fig. 80) consists of a simple thin-walled esophagus that opens into a rather large intestine. The mid-intestine narrows posteriorly into the hind-intestine at the point of entrance of the Malpighian tubules. The hind-intestine curves forward, then backward to the anal opening. There is a large rectal ampulla. The salivary glands consist of two pairs—a pair of tubular glands and a pair of kidney-shaped glands. Each gland has a duct that opens independently into the base of the diverticulum containing the mouth parts. Here they connect with the salivary duct lying between the stabbers.

LIFE CYCLE: Adult females of the head louse begin oviposition in from 24 to 36 hours after emergence from the last nymphal skin, and each lays, on an average, six to seven eggs a day. The total number of eggs produced by a single female does not seem to be definitely known though Bacot obtained a maximum of 141 eggs; Buxton (1946) reports an average of 270 to 300 eggs per female. The eggs are cemented to hairs (Fig. 81 A) and are practically always deposited with the cap directed away from the base of the hair. They measure from 0.9 to 1 mm. in length. The small, whitish eggs are usually known as "nits." The eggs hatch in from five to nine days when kept at temperatures (30° to 35° C.) normal to the habitat of the lice. When ready to emerge the nymph employs a novel method to open the lid or cap of the egg. Air is pumped in through the mouth parts and gradually extruded from the anus until a cushion of air is obtained of sufficient pressure to force open the cap. The fore part of the nymph, which has acted like a stopper, is forced out; pumping continues and the nymph is gradually forced out of the shell. The nymph begins feeding promptly within a few hours. There are three molts before the adult stage is reached. The length of the life cycle has been accurately determined by Nuttall and is as follows:

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[3] For a full and extended account of the mouth parts and their action the reader is referred to the works of Harrison, Sikora, Peacock, and Florence. The above account is necessarily brief and is abstracted largely from these workers.

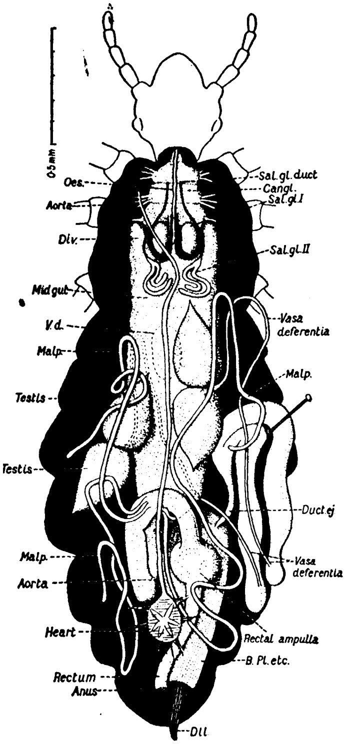
0.5mm
Oes.
Aorta
Dlv.
Midgut
V.d.
Malp.
Testis
Testis
Malp.
Aorta
Heart
Rectum
Anus
Sal.gl.duct
Cangl.
Sal.gl.I
Sal.gl.II
Vasa deferentia
Malp.
Duct.ej
Vasa deferentia
Rectal ampulla
B.Pl.etc.
Dil

Fig. 80 (*left*). *Pediculus humanus.* Internal anatomy of male louse; parts fully labeled. (After Nuttall, *Parasitology.*)

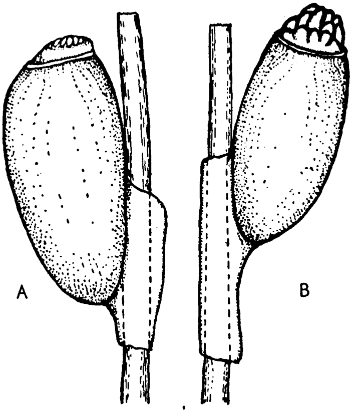

Fig. 81 (*right*). Eggs of human lice. (*A*) *Pediculus humanus.* (*B*) *Phthirus pubis.*

Egg stage	7 days
1st nymphal stage	4 days

2nd nymphal stage	3 days
3rd nymphal stage	2 days
Total	16 days

The length of the life cycle may be somewhat prolonged by low temperatures or lack of food. The adults live about 30 days.

THE BODY LOUSE: *Pediculus humanus* var. *corporis* de Geer,[4] the body louse, is found principally on the body and oviposits generally on the clothing. In practically all characteristics it agrees with *capitis,* though it averages slightly larger in size. About the only distinguishing characters are its habitat and its preference for laying its eggs on the clothing rather than on the hairs. Nuttall has shown that *capitis* will oviposit on cloth and that *corporis* will lay its eggs on the body hairs. Such eggs have been found naturally on the body hairs of persons infested with this louse. The life history of the body louse is very similar to that of the head louse. Nuttall has shown that the female lays from 275 to 300 eggs, ovipositing at the rate of about ten a day. The eggs hatch in from six to nine days and the entire life cycle from egg to egg may be as short as 16 days. The optimum temperature for its development is 30° to 32° C.

BIONOMICS OF LICE: FEEDING HABITS: The method of feeding has already been described. Whereas starved lice will gorge to excess, those present on the body feed whenever hungry. They feed most commonly at night or when the host is resting. The act of feeding usually occupies three to ten minutes (Nuttall), though other authorities record even as long as two or three hours, the lice sucking intermittently. The young lice begin feeding almost immediately after hatching, and, if conditions are favorable, continue to feed at varying intervals throughout life. As the lice feed and the intestine fills with blood, excreta are commonly voided in more or less profusion. This is a very important fact when the methods of transmission of pathogenic organisms are considered.

HABITAT: The head louse (*capitis*) is primarily an inhabitant of the head. It may occur and establish itself on other hairy parts, as the beard, pubic region, and chest. The body louse (*corporis*) is largely confined to the clothing on which it lays its eggs. Nuttall has recorded a severe infestation of *capitis* on the pubic region. Many observers record the presence of *corporis* on the body and the deposition of its eggs, though not commonly, on the hairs of the breast, axillae, perianal, and pubic regions. This is especially true when the infestation is severe. These observations are of great importance when delousing operations are considered. It is useless to delouse by change of clothing after an ordinary bath. If the eggs are present on the body hairs, the person will be soon as lousy as ever.

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[4] Under the rules of nomenclature this name should be *Pediculus humanus humanus* Linn.

ACTIVITIES: Lice are very active, crawling about with remarkable speed. Nuttall observed a female of *corporis* travel at the rate of one metre in three minutes, and it is evident lice can run a distance equal to the length of a man's body in a few minutes.[5] They have been seen wandering about rooms, crawling up walls, and, not uncommonly, moving about railway carriages and busses. They are more active when warm, *corporis* climbing more than twice as fast at 30° C. than at 17° C. At 0°C. they are immobile; at 10° C. they move slowly; at 20° C. they are fairly active; and at 30° C. they are very active (about the temperature of their normal habitat). At 38 ° to 40° C. they become wildly active and soon die from exhaustion. The thermal death point is about 44° C. (112° F.). Lice become very active on persons with fever, migrating from the patients in large numbers; when a person dies the lice soon abandon the body and scatter. These important facts should be remembered when attending persons suffering with relapsing or typhus fever.

Both the head and body lice are very gregarious, tending to congregate in large numbers in particular places. This habit may account for the density of a primary infestation before active spreading takes place. Nuttall has calculated that a single female may have 1918 descendants during her lifetime (about 30 days), and the offspring of her daughters, during their lifetime, would be 112,778, a rather large population to be produced in about 48 days.

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[5] It may be well to recall here the poem by Robert Burns entitled, "To a Louse, on seeing one on a lady's bonnet at church," in which he described very accurately the roaming activities of these creatures:

"Ha! where ye gaun, ye crowlin' ferlie!
Your impudence protects you sairly:
I canna say but ye strunt rarely,
Owre gauze and lace;
Though, faith, I fear ye dine but sparely
On sic a place.

. . .

"Now haud you there, ye're out o' sight,
Below the fatt'rils snug and tight;
Na faith ye yet! ye'll no be right
Till ye've got on it,
The very tapmost, towering height
O' Miss's bonnett."

MODES OF DISSEMINATION AND INFESTATION: It should be recalled that lice are very active, can attach easily to hair or cloth, and cling thereto very tenaciously; they can survive for a maximum of ten days without food. Lice can readily pass from head to head when in contact; lice, clinging to stray hairs, clamber quickly to any warm body surface near at hand; caps or hats worn by lousy persons and hung in close contact with others, as in schools and public places, undoubtedly serve to spread them. Hairs from lousy persons are often scattered in public conveyances, and these falling on other people's clothing may start an infestation. Persons suffering from head lice are constantly scratching, and hairs bearing nits (eggs) are continually dropping, frequently on seats and cushions of railway carriages, busses, etc. Probably the most common method of acquiring lice is through contact with infested clothing, bedding, brushes, etc.

THE CRAB LOUSE: *Phthirus pubis* (Linn.)., the groin, pubic, or crab louse (Fig. 82), is a very distinctive louse. It is usually confined to the pubic and perianal regions, though it is recorded from the head, eyebrows, eyelashes, the axillae, breast, and beard. Herms records seeing soldiers infested from their ankles to their necks, and Nuttall also observed similar conditions among soldiers he examined in England. However, the main site of infestation is the pubic and perianal region. The prevalence of this louse among the general population is not known. Greenough (1888) records that in the examination of 864 verminous patients admitted to a hospital in Boston 3 per cent were infested with the crab louse. From personal knowledge the author is led to believe that this louse is quite widely prevalent, but very few records are kept. It is restricted to man as a host, though there are some records of dogs being infested. Further investigation is needed to learn whether the dog may be a normal host and serve as an animal reservoir of this louse.

The crab louse is grayish white in color; it measures 1.5 to 2 mm. in length and is nearly as broad as long. It remains almost immobile upon the host, the hind legs grasping two hairs. In this position it continues to feed intermittently for hours or days, rarely removing its mouth parts from their position in the host. During its entire life it remains near its first point of attachment, withdrawing its mouth parts only at the time of molting. As it feeds it defecates frequently, voiding blood and wastes intermingled. This frequent defecation soon renders its surroundings filthy.

LIFE CYCLE: Nuttall gives an excellent account of the biology of this species. Mating takes place on the host and the eggs (Fig. 81 *B*) are deposited on the hairs, close to the base. The total egg production of a single female has not been accurately determined, though Nuttall records 26 eggs laid by one during a period of 12 days (the female died 17 days after reaching sexual maturity). The eggs hatch in from 7 to 8 days. The young nymph attaches within a few hours, and the first molt takes place in from 5 to 6 days; the second molt in 9 to 10 days; and the third molt in from 13 to 17 days. The complete life cycle from egg to egg occupies from 34 to 41 days. The nymphs or adults cannot survive very long when removed from the host, a maximum of two days being recorded.

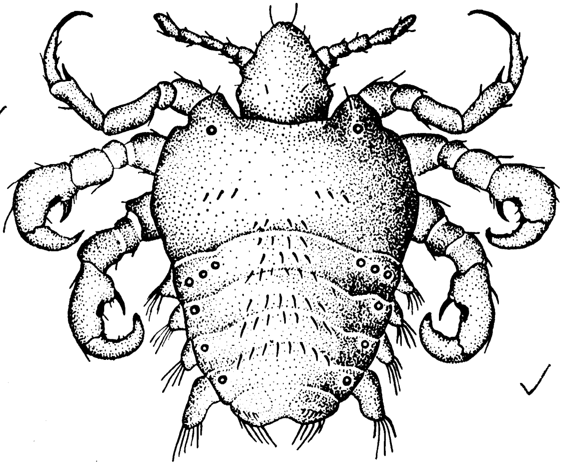

Fig. 82. The pubic louse, *Phthirus pubis.* Female.

DISSEMINATION: The crab louse is usually spread during coitus, but there are many other ways in which persons may become infested. Some of these are the use of common or piled bath towels in dormitories, gymnasiums, etc.; contact with hairs bearing eggs or lice that may drop on clothing, bedding, the seats of public toilets, etc., as the result of scratching by infested persons; the throwing or piling together of undergarments, athletic suits, etc. Under crowded conditions a single infested individual may distribute them to an entire family or group of people with whom he or she comes constantly in contact.

LICE AND DISEASE

HEAD AND BODY LICE

The head and body lice of man affect him in two principal ways: through the direct effects of their bites and by the transmission of pathogenic organisms.

BITES: The bites of lice have a very marked effect on most people, though some persons are apparently immune to their attacks (Moore and Hirschfelder record an experimental individual on which lice refused to feed) and others become immune after continued attack. The bites produce minute hemorrhagic spots, which are found most frequently over the neck, back, breast, and abdomen. These spots are accompanied by an urticaria, often with intense itching, leading to scratching and frequent secondary infection. Among persons (as tramps, vagabonds, chronic drunkards, and children living under filthy conditions) who harbor lice for years, the skin back of the head, over the breast, and on the neck, back, or any part frequently bitten becomes roughened, thickened, and deeply pigmented (melanoderma), producing what is commonly called "vagabonds' disease." As the body louse attacks most frequently at night or when the host is resting, it causes a great deal of irritation, loss of sleep, and restlessness, which may induce irritability and an anemic condition, especially in children. Insomnia and neurasthenia may result from continued infestation. Moore (1918) records rather severe effects from the experimental feeding of lice on himself. After feeding 700 to 800 lice twice each day, he developed almost at once a tired feeling, an irritable and pessimistic state of mind, and an illness resembling grippe with a body rash. All these effects rapidly disappeared when the lice were removed and feeding discontinued.

DISEASES: There are at least three important human diseases transmitted by lice: (1) epidemic typhus; (2) trench fever; and (3) relapsing fever. Another disease, endemic typhus or murine typhus, is mainly associated with rats and rat parasites, since fleas and mites are the transmitters among rats and to man (see pp. 98, 560); human lice are also capable of acting as vectors.

EPIDEMIC TYPHUS, OLD WORLD TYPHUS, JAIL FEVER, TYPHUS EXANTHEMATICUS, LOUSE TYPHUS, ETC.: Typhus is an acute infectious disease caused by *Rickettsia prowazeki* da Rocha-Lima (1916) and is transmitted by the human louse, *Pediculus humanus* Linn. The disease is characterized by sudden onset, high fever, severe headache, and marked prostration, followed on the fourth or fifth day by a pinkish body rash. The course of the disease is rapid, a fall in temperature occurring on the twelfth to the fourteenth day, followed by a rapid recovery or death. The mortality rate varies from 5 per cent to as high as 70 per cent in severe epidemics.

Typhus fever is world-wide in distribution and may occur wherever human lice are abundant. Epidemics have occurred in most parts of the world. It is prevalent principally in the cooler climates where people are compelled to wear heavy clothing and bathing and clothing changes are infrequent. Outbreaks are most frequent in the winter because of the crowding of the poorer classes, bad sanitary conditions, and lack of adequate food, inducing general debility. The disease is practically always associated with poverty and unsanitary living conditions or, under war conditions, with famine, national poverty, political upheavals, or revolutions. Severe epidemics occurred during World War I in Serbia, Romania, and Poland, and the aftermath witnessed severe outbreaks in Poland and Russia. In World War II epidemics threatened in areas overrun by the various armies as in Italy and North Africa, but these were soon halted by the use of DDT.

That lice are the transmitters of typhus was first demonstrated by Nicolle and his associates in 1909 in Tunis, North Africa. They succeeded in transmitting typhus from infected monkey to uninfected monkey by body lice. These results were fully confirmed by Ricketts and Wilder (1910), Goldberger (1912), and others in various parts of the world. These workers stated that the transmission was by the bites of the louse; this is now known not to be the case. The causative organism was discovered by da Rocha-Lima (1916), and the complicated method of transmission by lice has since been fully elucidated. Man is believed to be the reservoir of the disease. Lice feeding on typhus patients ingest the rickettsiae that are in the circulating blood during the febrile period (the third to the 10th day). In the lice the rickettsiae invade the epidermal cells lining the stomach and mid-gut; here they multiply in enormous numbers and cause the cells to burst and liberate them. This developmental cycle requires from five to nine days. The infected louse now feeds on a new patient and infection may occur in one of three ways: (1) the louse in feeding defecates and the rickettsiae in the feces may enter the wound or the abrasions that result from scratching; (2) the louse is crushed by the patient and the contents of the intestine of the louse are spread over the skin to enter wounds or scratches; (3) the feces of infected lice may fall on mucous membranes about the eyes, the mouth, or other exposed mucous surfaces. In addition, it has been demonstrated that, though infected feces may become dry and powdery, the rickettsiae are still infective and may be scratched into the skin or rubbed on mucous surfaces or they may be air-borne and gain access to mucous surfaces (from feces contaminating bedding, clothing, and so forth).

The rickettsiae in man invade the cytoplasm of the cells, and the incubation period varies from 8 to 12 days. No successful treatment is known. At present a fairly effective vaccine has been developed from killed rickettsiae and is being used with considerable success. The prevention of infection is of the greatest importance in controlling or preventing an outbreak. This involves effective louse control (see pp. 211–213), cleanliness, improved living conditions, adequate bathing and laundering facilities, and the prevention of louse-infected people from entering the areas. Mass vaccination is of importance where it can be done effectively. There is no known animal reservoir of epidemic typhus except man. However, the monkey lice (*Pedicinus longiceps* and *P. albidus*) have been shown capable of transmitting the disease to monkeys and the rat louse, *Polyplax spinulosa,* of transmitting the disease among rats. The rickettsiae are not known to be transmitted by lice to their young (in fact most infected lice are said to die). The sources of epidemic outbreaks are not known.

BRILL'S DISEASE: Although generally regarded as a form of murine or endemic typhus, Brill's disease has been shown to be a mild form of epidemic typhus and is transmitted by the human louse.

ENDEMIC TYPHUS, MURINE TYPHUS, OR FLEA TYPHUS: This is a mild typhuslike disease caused by *Rickettsia mooseri* (*typhi*) and is transmitted to man by the bites of infected fleas, infective flea feces, or the eating of food contaminated by urine from infected rats. The body louse, *Pediculus humanus corporis,* can also transmit the disease.

That rats (the brown rat, *Rattus norvegicus,* and others) and probably mice are the reservoirs of the rickettsiae has been well demonstrated by Dyer, Rumreich, and their associates (1931, 1932), Mooser and his co-workers in Mexico, and many others. More recently Brigham (1937) has isolated a strain from a field mouse (*Peromyscus polionotus polionotus*) from a rural district in southern Alabama, and the same author (1937) has shown mice, various species of rats, flying squirrels, cotton mice, golden mice, and wood rats to be susceptible to infection. Among rats the vectors are fleas (*Xenopsylla cheopis, Nosopsyllus fasciatus,* and probably others), the rat louse (*Polyplax spinulosa*), and the tropical rat mite (*Liponyssus bacoti*). Brigham (1941) recovered a strain of typhus from the sticktight flea, *Echidnophaga gallinacea,* collected from rats in Georgia, and Alicata (1942) transmitted endemic typhus by this flea.

The disease in man (apparently it has little effect on rats or other rodents) is mild, and the death rate is less than 5 per cent in the United States. In man the incubation period varies from 6 to 14 days followed by fever and a rash. Recovery normally occurs in two or three weeks. Eskey (1943) reports some 20,000 cases in the United States from 1932 to 1941 but indicates that this was probably less than 20 per cent of the actual cases. As the main source of human infection is rats, the control or eradication of these pests would practically eradicate the disease.

Murine typhus is widely distributed in the southern United States, extending northward into New York, Ohio, Iowa, and California; it is widespread in Mexico, parts of South America, Africa, southern and western Europe, the Near East, eastern Asia, and nearby areas.

TRENCH FEVER: Trench fever, or Volhynia fever, was first diagnosed as a clinical entity in 1915 during World War I. It is believed to be caused by *Rickettsia quintana* (*R. wolhynica*), but this has not been definitely proved. It is a specific relapsing fever transmitted to man by the body louse, *Pediculus humanus corporis,* through the infected feces only. It is not transmitted by the bites of infected lice, nor is it known to be transmitted through the eggs. During World War I trench fever is said to have caused about 25 per cent of all cases of illness in the British Army in France and the disease was very prevalent in the German and Austrian Armies. Byam (1923) reports 800,000 cases among the Allied armies in France during the four years of the war. Outbreaks occurred in Egypt and Mesopotamia as well as in Europe. During World War II the disease was rare.

In man the organism of trench fever is present in the blood, and the blood is infective to lice from the first day of the disease. In lice there is a development period of five to nine days before the excreta are infective. The louse remains infective as long as it lives. The excreta retain their virulence for a long time, at least four months. Man becomes infected by scratching the excreta into the injured skin, crushing the lice, or in any way that brings the infective fecal wastes into the blood stream. In man the incubation period varies from 10 to 30 days (Mackie *et al.,* 1945). The onset is sudden with severe headache, weakness, vertigo, and fever of 103° to 104° F. The fever soon subsides (one to two weeks) and is followed by several relapses (three to five). During the disease there is usually a rash on the chest, back, and abdomen. Recovery is slow (frequently prolonged) and the sequelae are, in many cases, serious. As there is no successful treatment, the control of lice is very important. In man there is only a fleeting immunity and reinfection may occur within six months.

RELAPSING FEVER: There are two types of this disease, tick-borne (see pp. 71–73) and louse-borne. Species of *Spirochaeta* are the causative agents of the disease, but no agreement seems to have been reached as to the species concerned. *Spirochaeta recurrentis* (Lebert) is usually regarded as the louse species. There is doubt about the possibility or probability that tick-borne species can also be transmitted by lice or vice versa. The two diseases, typhus and louse-borne relapsing fever, frequently occur about the same time in the same areas, or they may be separated by a few years. Mackie (1907) first demonstrated that the body louse (*Pediculus humanus corporis*) served as the vector in India in an area where typhus had never been recorded. This work was confirmed by many investigators in North Africa and other parts of the world. According to Chung and Feng (1936), the developmental cycle in the louse is as follows. The louse feeding on a patient obtains the spirochetes in its blood meal. Most of the ingested spirochetes are soon digested, disappearing within six to eight hours. A few, however, penetrate the wall of the intestine and appear in the coelomic fluid in about two hours, and numbers are seen within eight hours. At the same time dead spirochetes appear in the feces. Within the body cavity the spirochetes multiply by transverse division and soon appear in all parts of the body. They do not invade the tissues nor are they transmitted through the egg or through the feces. Within the louse the spirochetes persist as long as the louse lives (19 days or more). Infection of man takes place by crushing the lice directly on the skin by the fingers or other means, whereby the spirochetes gain entrance through abrasions, or by scratching, thus permitting their access to the blood. The vectors are both the body and head lice.

Relapsing fever has occurred in epidemic form in most parts of the world. It is associated with lousiness in jails, armies, overcrowded and poverty stricken areas, famines, wars, and political disturbances. Though the clinical entity of the disease was recognized in the early part of the nineteenth century, it was not till 1873 that the etiological agent was described by Obermeier and named *Protomycetum recurrentis* by Lebert in 1874, now called *Spirochaeta recurrentis* (Lebert). Epidemics have been recorded from many countries and cities as in Dublin (1739 and later), parts of Scotland (1842–1844 and later), England (1847–1848 and later), Russia (1833, 1863, and later), Germany (1868 and later), most of Asia, Egypt (1851, 1884, and later), most of India (1852 and later), North Africa, West, central, and parts of East Africa (to the present time) and China; it is not known from Australasia. The disease has been recorded from the eastern coastal cities of North America (1844, 1847, 1871) but is apparently absent at the present time. It also occurs in some parts of South America.

During and after World War I great epidemics swept over Poland, central Russia, Romania, and Serbia. In Romania alone there were over one million cases of typhus and more of relapsing fever in a population of five million. The most recent great epidemic swept over central Africa, appearing first in French Guinea in 1921, and gradually spread southward to Nigeria, eastward to the Anglo-Egyptian Sudan, and northward to various areas. By 1928 it had subsided, though during the epidemic it is estimated about 10 per cent of the population died. In French Sudan and the Niger area over 80,000 died within two years. (Scott, 1939). Though some of the newer arsenical drugs appear to act effectively in the cure of relapsing fever, yet the most important measure is the control of lice. Where lice are adequately controlled, louse-borne diseases soon disappear.

OTHER LICE

Phthirus pubis has not, apparently, been extensively experimented with as an agent in the transmission of disease. "It is not known to serve as a vector of any infective disease" (Nuttall, 1918). Todd (1922) states that it may transmit relapsing fever. The main effects of this louse are local. Pruritus is usually the first symptom and leads to scratching and secondary infections. With many persons no ill effects are evident though pale bluish-gray maculae mark the sites of the bites.

Another interesting relation of lice (other than human lice) to man is that a species of dog lice, *Trichodectes canis* de Geer[6] (a species of *Mallophaga*), serves as the intermediate host of the dog tapeworm (*Dipylidium caninum* Linn.). This tapeworm is found occasionally in man, particularly children. The dog harbors the tapeworm, and the defecated proglottids with their eggs become entangled in the hairs of the host. If these eggs are devoured by the lice, the cysticercoid stage develops in them. The dog becomes infected by swallowing the infected lice. Persons handling and petting infected dogs may accidentally become infected through swallowing a louse containing the cysticerci. This most commonly occurs with children that play with dogs harboring this species of tapeworm.

Another interesting relation is that of the rabbit louse, *Haemodipsus ventricosus* Denny (Siphunculata). Francis (1921) showed experimentally that this louse is an active agent in the dissemination of tularemia (*Bacterium tularense*) from rabbit to rabbit. This is undoubtedly one of the means by which this disease is transmitted in nature, and it thus aids in maintaining a natural reservoir from which man may become infected.

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[6] Other intermediate hosts are the dog and cat fleas (*Ctenocephalides canis* and *C. felis*) and the human flea (*Pulex irritans*).

CONTROL OF LICE

The problem of the control of lice may well be discussed under two distinct heads: (1) personal cleanliness and delousing; (2) public cleanliness and mass delousing.[7]

DELOUSING OF THE INDIVIDUAL

PERSONAL CLEANLINESS: Personal cleanliness is probably the most effective measure against lousiness. However, the religion of cleanliness, both personal and public, has not become universal, and there still exists, among all peoples and nations, a proportion of the population that may be called "the great unwashed." Unfortunately, cleanliness is not always a concomitant of what may be called a rising civilization. Furthermore, there are many superstitions in regard to lice, their presence being taken to indicate good health, vigor, fertility, protection against disease,[8] etc. Owing to the dangers of disease transmission, everyone should take the utmost precaution against infestation. Certain simple rules should be followed as far as possible: (1) avoid all contact with lousy persons and their effects; (2) avoid overcrowding whenever possible; (3) bathe at least once a week, using plenty of hot water and soap, and rub dry with a rough towel; (4) wear underwear at all times and make a complete change at least once each week; to use no underwear is an unclean habit and invites lousiness; (5) wash the head carefully at frequent intervals; comb and brush it at least once a day and keep it clean at all times; (6) avoid unclean bedding, especially blankets; when traveling, carefully inspect the bedding before retiring; (7) carefully inspect the head and body at frequent intervals, especially if you have been exposed to contacts with lousy individuals; (8) in case of infestation, vigorous treatment should be adopted at once.

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[7] Lousing is the correct term to use in this connection but it has fallen into disuse, owing, no doubt, to the decreasing lousiness of peoples. To louse, according to the *Oxford English dictionary,* means "to clear of lice, to remove lice." "Howe handsome it is to lye and sleepe, or to lowze themselves in the sunshine" (Spenser, *View of the Present State of Ireland,* 1633). "To York House, where the Russian Ambassador do lie; and there I saw his people go up and down lousing themselves" (Pepys' *Diary,* June 6, 1663). (From Nuttall.)

[8] "Ten lice boiled in milk with plenty of salt and taken on an empty stomach was certain to cure jaundice, a very common complaint among the Lapps in Spring" (*The Story of San Michele* by Axel Munthe).

HEAD LICE (*P. humanus capitis*): In mild infestations the lice and the nits (eggs) can be removed by hand picking and vigorously combing with a fine-toothed comb. Frequent washing and combing will usually eliminate a mild infestation. If lice are abundant or even if only a few, they can be quickly destroyed by one of the newer lousicides. A 10 per cent DDT (by weight) in some carrier as pyrophyllite is very effective. Dust the head thoroughly (about a spoonful of the powder) and rub the dust in vigorously with the hands. Also rub some into the eyebrows and beard (if present); avoid getting any into the eyes. The head should not be washed for 24 hours or longer. This will kill all the lice but not the eggs. Use the same treatment a week or ten days later to kill any lice that have hatched. Two thorough treatments even on heads with dense hair will eliminate lice. Another treatment is by the use of liquid solutions of DDT. When using these, follow carefully the directions of the manufacturer as given on the containers.

BODY LOUSE (*P. humanus corporis*): As this louse is found mainly on the clothing, a thorough treatment of the clothing, especially the underwear, is the most effective method. Sift a 10 per cent DDT powder thoroughly over the insides of the underwear, carefully rubbing it into all the seams. Apply the same treatment to the insides of trousers (in the case of women, treat the insides of skirts), shirts, and caps. If such garments are worn without washing, a single treatment is good for three weeks. If washed in warm soapy water, the clothing will still be effective for a short period. If new infestation is avoided, a single treatment should be effective. In case of constant exposure to infestation, as on the part of nurses, social workers, medical officers, or others working among lousy persons, especially when typhus or relapsing fever is prevalent, the underclothing may be impregnated with a DDT emulsion or DDT may be mixed with a dry-cleaning fluid. Such emulsions can be prepared or purchased.

CRAB LOUSE (*Phthirus pubis*): This louse may be controlled by dusting the groin region, the arm pits, or other hairy portions of the body with a 10 per cent DDT dust. Rub in thoroughly and do not bathe for at least twenty-four hours. Follow with a second treatment in a week to ten days to kill any lice that have hatched.

*

MASS DELOUSING

In armies or among lousy populations it is often necessary to use mass delousing methods. These methods were developed and refined during World War II. The simplest method used in Naples, Italy (1943–1944), to control an epidemic of typhus was the use of DDT as a 10 per cent dust (by weight). By means of small hand blowers the dust was blown between all layers of the clothing, particular attention being paid to undergarments. This was accomplished by blowing down the back, down the front, up the sleeves, down the trouser legs, and up the legs to cover the entire body and clothes with the dust. If such dusted clothing is worn for a week or longer, all the lice and those hatching from eggs will be destroyed. Such a mass delousing can be carried out effectively only under police regulations acting under the orders of the medical authorities.

To carry out a mass delousing program requires legal regulation, for it necessitates not only destroying the lice on the persons but also those on discarded or recently worn clothing. This may be carried out effectively by organizing definite delousing stations, as is done by the Army and Navy and at ports of entry to any country. In such a station arrangements are made that all worn clothing in addition to those on the individual must be brought. All such clothing, including what is worn, is placed in a gastight bag in which is placed the required amount of methyl bromide in glass ampoule, or the clothing is labeled and placed in gastight chambers for treatment with methyl bromide. In the bag the ampoule is broken, and in 45 minutes the bag may be opened and the clothes taken out and shaken. They are now ready for wear. In the gas chambers masses of clothing can be treated. While the clothing is being treated, the unclothed individuals may take a bath. They are then sprayed with a lousicide such as the NBIN formula (see p. 103) used by our Army and Navy. The individual now receives his clothing, all the lice on his body and his clothing having been killed. By such a method 400 to 500 can be treated each day in a small station; larger units can handle more. In addition, mobile units can be used where isolated groups have to be treated.

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CHAPTER VIII

The Diptera: Flies

THE Diptera are insects with only one pair of membranous wings (in some groups the wings are lacking or vestigial) which are borne by the mesothorax (Fig. 83); the second pair of wings is represented by a pair of short, knobbed, filiform organs, the halteres (Fig. 53). The mouth parts are suctorial, usually forming a proboscis and, in some groups, adapted for piercing. The larvae are legless and their respiratory system is reduced (generally amphipneustic); the pupae are usually free or enclosed in the last larval skin (puparium). The metamorphosis is complete.

The Diptera constitute a very large order: over 80,000 species have been described from the world and at least 10,000 from North America. Many of the species are very abundant in individuals and are world-wide in distribution. Furthermore, they vary extremely in their habits both as larvae and as adults. The adults are mainly diurnal, feeding on nectar, the exudates from plant and animal wounds, or decaying animal or vegetable matter; some are predaceous, as the robber flies (Asilidae), while large groups, and sometimes almost entire families, have acquired the bloodsucking habit and attack a great variety of hosts. The larvae may be scavengers, as the blowflies, flesh flies, bluebottle flies, etc., parasites on man and animals, as in the myiasis-producing flies (see pp. 492–533), or parasites on other insects (all the Tachinidae, some of the Sarcophagidae, etc.). Many are injurious to man's crops; others are beneficial, destroying noxious insects (the larvae of the Syrphidae are usually predaceous and feed on a great variety of insects; those of the Tachinidae are also beneficial); while many others feed on wastes of all kinds and, in many cases, are highly beneficial.

The bloodsucking habits of the adults; the propensity of many flies to feed on fecal or decaying wastes and human and animal foods; their search for moisture on mucous membranes, exudates from sores, wounds, or discharges from diseased tissues; and the domestic habits of many species—all render the group of great importance to man. In addition to these extremely annoying habits, many flies, both bloodsucking and nonbloodsucking, are now known to be the vectors or hosts in the developmental stages of many parasites pathogenic to man and animals. Here may be mentioned mosquitoes and malaria, yellow fever, dengue, filariasis, encephalitis (and other diseases); *Glossina* flies and sleeping sickness or trypanosomiasis; houseflies and typhoid fever, diarrheas, (and other diseases); *Phlebotomus* flies and Oroya fever, kala azar, and pappataci fever. Viewing the group as a whole we may roughly classify the disease relationships of flies to man and animals in the following categories:

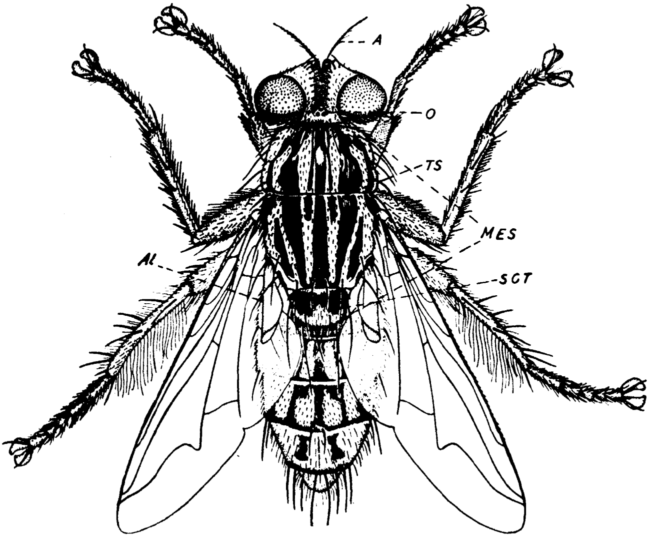

Fig. 83. A common flesh fly, *Sarcophaga bullata.* A, arista of antenna; Al, axillary lobe; MES, mesonotum, which occupies practically all of the dorsal surface of the thorax; O, ocelli; SCT, the scutellum of the mesonotum; TS, transverse suture.

1. Flies, bloodsucking in habit, act as carriers of pathogenic organisms. The carriage may be mechanical, that is, the fly feeding on the blood of a diseased animal may go directly to another susceptible animal to complete its meal and inoculate living organisms present in or on its proboscis; the fly may also act as a host in the developmental cycle of the organism, as mosquitoes do in malaria.

2. Flies, nonbloodsucking in habit, may deposit their eggs or living larvae in wounds, sores, cavities, on the surface or hairs of the body, or on food, and the

larvae developing cause serious diseased conditions (myiasis-producing larvae).

3. Bloodsucking and nonbloodsucking flies may act as the intermediate hosts of helminths of man and animals. Examples: *Culex fatigans* and *Wuchereria bancrofti* of man; *Culex pipiens, Aedes vexans,* etc., and *Dirofilaria immitis* of dogs; *Simulium damnosum, S. metallicum,* and *Onchocerca volvulus* of man; *Chrysops* spp. and *Loa loa* of man; *Musca domestica* and *Choanotaenia infundibulum* of poultry; and many others.

4. Nonbloodsucking flies that seek moisture about mucous membranes, either diseased or not, or that feed on fecal or other human or animal wastes, liquids, or discharges from wounds may distribute pathogenic organisms on their bodies or by way of their intestinal tracts. The organisms obtained with the food may be digested but, if not, may be passed with the feces or the so-called "vomit spots" of many flies. A large number of flies are involved in these relations and our knowledge of them is far from complete.

STRUCTURE

The structure of the Diptera can be dealt with only very briefly, and then only those characters mainly concerned with classification and in the transmission of disease can be treated.

THE HEAD (Figs. 83,84): In flies the head is free and movable and usually of relatively large size. It bears the large compound eyes which may be contiguous on the vertex (holoptic) or widely separated (dichoptic). Ocelli are generally present and usually three in number, located between or slightly behind the eyes on the vertex. The antennae are of varied forms (Fig. 51) and furnish excellent characters for classification. The mouth parts are formed for sucking (Fig. 47), lapping, or piercing (Fig. 97). Their structure varies greatly in the different families and details will be given in the treatment of those families (for a general account see pp. 133–139). In the specialized Diptera (suborder Cyclorrhapha) there will be observed a small inverted U-shaped suture immediately above the antennae, the frontal suture (Fig. 84). This suture represents the opening through which the ptilinum, a bladderlike structure, was extruded at the time the adult emerged from its puparium. The ptilinum is forced out by internal pressure and the cap of the puparium is broken off; its usefulness now ended, it is withdrawn into the head and the frontal suture marks the point of withdrawal. The median area extending from the frontal suture to the ocelli and lying between the rows of bristles (frontal bristles) is the frontal vitta. A small area above and between the bases of the antennae is known as the frontal lunule.

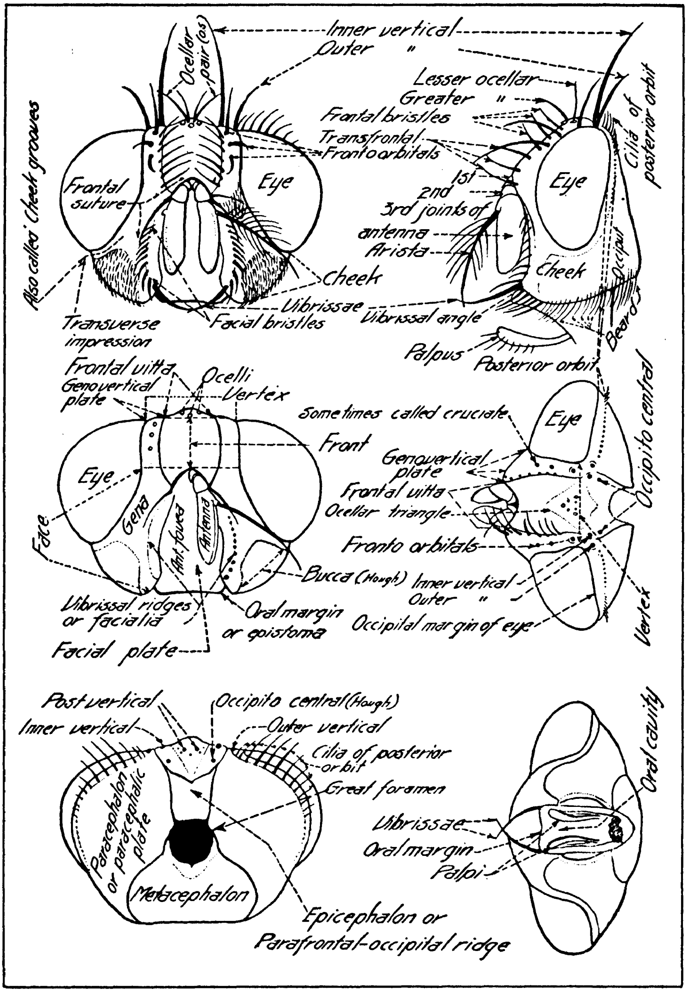
Inner vertical
Outer "
Ocellar pair (os)
Also called 'Cheek grooves'
Lesser ocellar
Greater "
Frontal bristles
Transfrontal
Frontoorbitals
Cilia of posterior orbit
Frontal suture
Eye
1st
2nd
3rd joints of antenna
Arista
Eye
Occiput
Cheek
Cheek
Vibrissae
Vibrissal angle
Beard
Transverse impression
Facial bristles
Palpus
Posterior orbit
Frontal vitta
Ocelli
Genovertical plate
Vertex
Sometimes called cruciate
Eye
Occipito central
Front
Genovertical plate
Eye
Frontal vitta
Ocellar triangle
Gena
Ant. fovea
Antenna
Face
Fronto orbitals
Bucca (Hough)
Inner vertical
Outer "
Vibrissal ridges or facialia
Oral margin or epistoma
Occipital margin of eye
Vertex
Facial plate
Post vertical
Occipito central (Hough)
Inner vertical
Outer vertical
Oral cavity
Cilia of posterior orbit
Great foramen
Paracephalon or paracephalic plate
Vibrissae
Oral margin
Palpi
Metacephalon
Epicephalon or
Parafrontal-occipital ridge

Fig. 84. The areas and setae of the head of the blowfly, *Calliphora viridescens.* (After Walton.)

THE THORAX: the thoracic region is largely composed of the mesothorax, both the prothorax and metathorax being greatly reduced (Fig. 85). The interpretation of the various sclerites of the thoracic region is still much in dispute so that conventional terms, with no special morphological value, are widely used. This is especially true of the terms used to designate the various groups of bristles or macrochaetae (Fig. 85). The wings of the Diptera consist of a single pair, the second pair being reduced and represented by the halteres. The wings are thin and membranous, usually naked or with microscopic setae. In the Psychodidae (moth flies) the wings are covered with fine hairs, while in the Culicidae (mosquitoes) the margin of the wing bears a fringe of scales and most of the veins are also scaled (Fig. 93). The venation of the wings is much used in the classification of this order. It corresponds rather closely to the hypothetical type (Fig. 55). The names applied to the veins and the cells will be found on pages 145–149. Fig. 86 shows in detail the modifications found in the more specialized Diptera (Muscidae) with all the veins and cells fully labeled.

In many families the posterior margin of the wing, near its base, is notched, the axillary incision; the lobe thus somewhat detached is called the posterior or axillary lobe (Fig. 86). In addition, the axillary lobe may be greatly expanded (many muscoidean flies) and folded beneath the wing base. When fully developed there are two extra lobes, one above the other (Fig. 83). These lobes are called the calypteres, alulae, or squamae, and are designated the upper and lower respectively.

The legs vary greatly in length and stoutness. They consist of the usual parts (Fig. 54). The tarsi are usually five-jointed and may terminate in pulvilli. Between the pulvilli there often exists a third structure, the empodium, which may be bristlelike or padlike.

From the standpoint of taxonomy the wing venation, antennal characters, and the arrangement of the bristles of the head, thorax, and at times the abdomen constitute very essential characters. The arrangement of the bristles are of especial importance in many of the groups of Diptera that are of great interest to the medical entomologist.

CHAETOTAXY OF THE DIPTERA

Muscoidean Flies (Myodaria)

THE HEAD:

The arrangement of the bristles and the parts on which they occur are fully illustrated in Fig. 84. A frontal view and a lateral view of the head are shown in the two upper figures and all the bristles are named. These are:

1. Facial Bristles: A series of bristles on each side borne by the vibrissal ridge, above the vibrissae.

2. Frontal Bristles: A row of bristles on each side of the frontal vitta; the lower ones directly above the frontal suture or base of the antennae are often called the *transfrontals;* and the upper one to four, the *frontals.*

3. Fronto-orbital Bristles: One or several bristles, usually in a row, between the frontal bristles and the eye. They are located on the genovertical plate.

4. Lateral Facial Bristles: One or two bristles at times present on the sides of the face below the eye (marked "sometimes called cruciate" in the figure).

5. Ocellar Bristles: A pair, the *greater ocellars,* are situated on the ocellar triangle just back of the median ocellus; they always point forward and diverge. The *lesser ocellars* are small bristles located in lines back of the greater ocellars and consist of a variable number.

6. Vertical Bristles: Two pairs, an *inner* and *outer* pair, situated on the vertex and inserted more or less behind the upper and inner corners of the compound eye.

7. The Vibrissae: A pair of stout bristles, one on each side of the lower part of the face, near or above the oral margin.

8. The Beard: The beard is represented as a mass of fine bristles present on the lower portion of the occiput and cheek.

9. The Arista: A prominent bristle, arising from the third segment of the antennae. It may be bare, partially or completely plumose, or modified in other ways (Fig. 51).

The parts of the head on which the above-described bristles are borne are fully explained in the figure.

THE THORAX (Fig. 85)

THE SUTURES AND REGIONS: The following sutures of the thorax are of importance in determining areas of the thorax:

1. The Transverse Suture is an impressed line extending across the mesonotum, terminating a little in front of the root of the wing.

2. The Notopleural or Dorsopleural Suture extends from the humeral callus to the mesopleural suture and separates the mesonotum from the pleuron.

3. The Mesopleural Suture extends downward from in front of the wing to the sternopleural suture, separating the mesopleuron from the pteropleuron.

4. The Sternopleural Suture separates the mesopleuron from the sternopleuron.

The areas bounded by these sutures are all named in the lateral view of the thorax (Fig. 85).

THE THORACIC BRISTLES: The bristles of the thorax and their arrangement are of great importance and a mastery of them is essential for any systematic work with the higher Diptera. Their importance is also accepted in other groups (Culicidae, etc.). The more important bristles are:

1. Acrostichals: Two rows of bristles, one on each side of the median line of the mesonotum. The transverse suture separates them into the anterior and posterior acrostichals.

2. Dorsocentrals: A row on each side, next to and parallel with, the acrostichals. The transverse suture divides them into the anterior and posterior dorsocentrals.

3. Discal Scutellars and *Marginal Scutellars:* The discal scutellars usually consist of a pair of bristles on the dorsal portion of the scutellum; the marginal scutellars form a distinct row of large bristles on the margin of the scutellum.

4. The Humerals: One or more bristles situated on the humeral callus.

5. The Hypopleural Row: A row of bristles running in a more or less vertical direction on the hypopleura (usually directly below the posterior spiracle or above the hind coxa). The bristles may be grouped in a tuft.

6. The Intra-alars: A row of two or three bristles just laterad of the posterior dorsocentrals.

7. The Mesopleural Row: A prominent row of bristles in front of the mesopleural suture and below the dorsopleural suture.

8. The Notopleurals: Usually two bristles inserted directly above the dorsopleural suture, between the humeral callus and the root of the wing.

9. Post-alars: Bristles on the post-alar callus directly back of the supra-alar row and the intra-alars.

10. Post-humerals: Two or three bristles located just behind the humeral callus on the mesonotum.

11. Prescutellar Row: A name applied to the row of bristles just in front of the scutellum and consisting of the caudal dorsocentrals and acrostichals.

12. Presuturals: One or more bristles just in front of the outer end of the transverse suture and above the presutural depression.

13. The Sternopleurals: One or several bristles on the sternopleura and directly below the sternopleural suture. These are often arranged two in

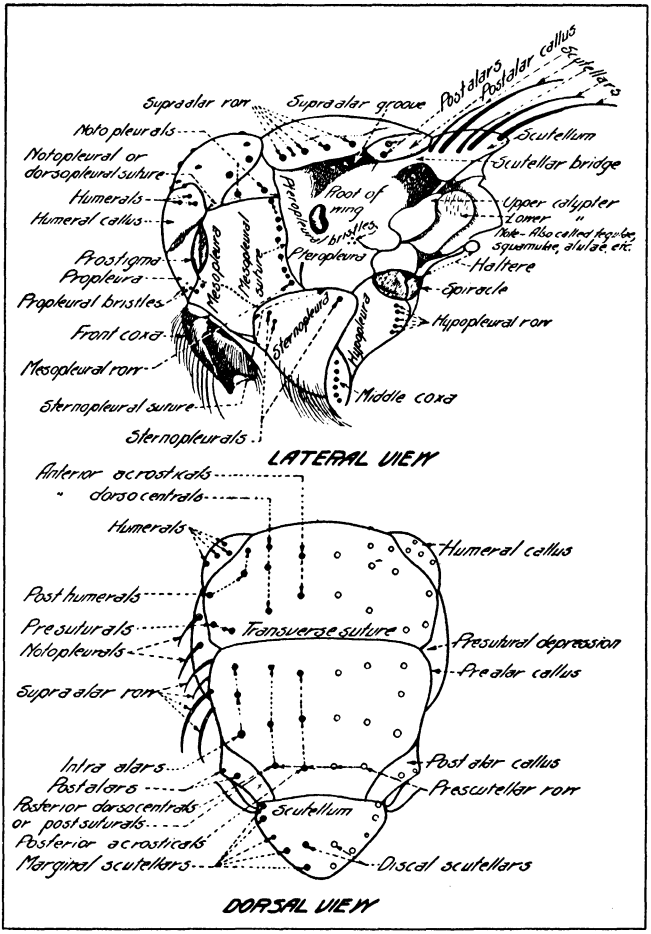
Supraalar row
Supraalar groove
Postalars
Postalar callus
Scutellars
Noto pleurals
Notopleural or dorsopleural suture
Scutellum
Scutellar bridge
Humerals
Humeral callus
Root of wing
Pteropleural bristles
Upper calypter
Lower "
Note - Also called tegulae, squamulae, alulae, etc.
Mesopleura
Mesopleural suture
Pteropleura
Prostigma
Propleura
Haltere
Propleural bristles
Spiracle
Sternopleura
Hypopleura
Hypopleural row
Front coxa
Mesopleural row
Middle coxa
Sternopleural suture
Sternopleurals
LATERAL VIEW
Anterior acrostichals
" dorsocentrals
Humerals
Humeral callus
Posthumerals
Presuturals
Transverse suture
Notopleurals
Presutural depression
Prealar callus
Supraalar row
Intra alars
Postalar callus
Postalars
Prescutellar row
Posterior dorsocentrals or postsuturals
Scutellum
Posterior acrostichals
Marginal scutellars
Discal scutellars
DORSAL VIEW

Fig. 85. The principal external structures of the thorax of the blowfly, *Calliphora viridescens,* and the arrangement of the macrochaetae. (After Walton.)

front and one behind (written "sternopleurals 2:1"); one in front and two behind (1:2); two in front and two behind (2:2); etc.

14. The Sub-lateral Row: Frequently the anterior posthumerals and the inner presutural are treated as a row and bear the above name.

15. The Supra-alar Row: Usually one to four bristles in a row above the root of the wing between the notopleurals and the post-alars.

CLASSIFICATION OF THE DIPTERA

The Diptera are divided into two suborders, the Orthorrhapha or the straight-seamed flies and the Cyclorrhapha or the circular-seamed flies.

The Orthorrhapha includes those flies in which the pupa escapes from the last larval skin through a transverse or T-shaped slit near the anterior end, or by a transverse slit between the seventh and eighth abdominal segments. The larva usually has a well-developed or somewhat reduced head. The pupa is naked, never enclosed in the last larval skin. The adults are either slender flies with long and many-jointed antennae or robust flies with reduced antennae. The venation of the wing is simple (Figs. 56,57).

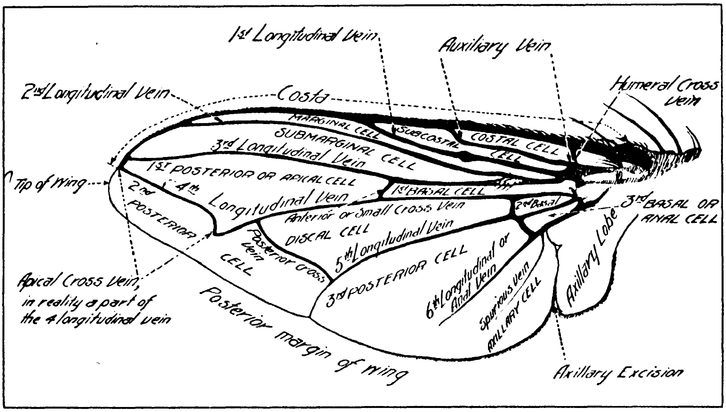
1st Longitudinal Vein
Auxiliary Vein
2nd Longitudinal Vein
Costa
Humeral Cross Vein
MARGINAL CELL
SUBCOSTAL
COSTAL CELL
SUBMARGINAL CELL
CELL
3rd Longitudinal Vein
Tip of Wing
1st POSTERIOR OR APICAL CELL
4th Longitudinal Vein
1st BASAL CELL
2nd POSTERIOR
Anterior or Small Cross Vein
2nd Basal
3rd BASAL OR ANAL CELL
DISCAL CELL
Posterior Cross Vein
CELL
5th Longitudinal Vein
3rd POSTERIOR CELL
6th Longitudinal or Anal Vein
Spurious Vein
AXILLARY CELL
Axillary Lobe
Apical Cross Vein, in reality a part of the 4 longitudinal vein
Posterior margin of wing
Axillary Excision

Fig. 86. Wing of *Calliphora viridescens* (= *C. livida*) with veins and cells labeled. (After Walton, *Entomological News.*)

The Cyclorrhapha include those flies in which the pupa is not naked but is enclosed in the last larval skin—the puparium. The adult emerges through a round opening made by pushing off a cap at the anterior end by means of the ptilinum. The adults possess a frontal lunule that is delimited by the frontal suture (Fig. 84). The wing venation is more complicated (Fig. 86).

SUBORDER ORTHORRHAPHA

This suborder is divided into two series that are difficult to differentiate as there are no well-defined and clear-cut separating characters.

SERIES I, NEMOCERA (Nematocera): In this series the larva possesses a well-developed head with mandibulate mouth parts; the pupa is free, not enclosed in the last larval skin. The adults have long antennae, many-jointed (8 to 16 or more), usually longer than the head and thorax, and the joints nearly similar; the palpi are pendulous, consisting of one to five segments. The anal cell (1st A) is not narrowed toward the margin of the wing and the discal cell is generally absent (Fig. 86).

The Nemocera include some twelve or more families of flies. Only four of these families contain species known to be of medical importance; in two of these families only a small group of species is of significance.

SERIES II, BRACHYCERA: In this series the larval head is usually reduced, generally retractile, the mandibles acting vertically instead of horizontally; the pupa is free. The antennae are shorter than the head and thorax, generally three-jointed; the last segment is elongate and often annulate; style or arista, when present, is terminal, palpi are porrect, one- or two-jointed. Discal cell usually present and the anal cell is closed or narrowed before the margin of the wing (Figs. 56,57).

THE SUBORDER CYCLORRHAPHA

This suborder includes a large number of families. Their classification is in a very unsatisfactory condition since well-defined differentiating characters have not been found. At present the suborder is divided into two series, the Aschiza and the Schizophora.

SERIES I, THE ASCHIZA: In this series the adults do not possess a frontal suture, or it is restricted; the ptilinum is nonpersistent, not being retained after the adult emerges from the puparium. The series contains four families of which one, the Syrphidae or hover flies, is of medical importance (see pp. 524–527).

SERIES II, THE SCHIZOPHORA: The adults possess a frontal suture, well marked, and the ptilinum persists as a structure retained within the head, directly behind the suture. This series is composed of a large number of families, many of them of the greatest interest to the medical entomologist. It is generally divided into two sections, the Myodaria and the Pupipara.

Section I, *Myodaria:* The Myodaria or muscoidean flies is the largest group of Diptera, including many families and probably more than half of all the living species of flies. This section is further divided into two subsections, the Acalypteratae and the Calypteratae.

In the Acalypteratae the squamae or calypteres are small or vestigial and do not conceal the halteres; the transverse suture of the thorax is usually not distinct. This group contains many families of small, to very small, flies; a few are of importance to man and are discussed on pages 527–528.

In the Calypteratae the squamae or calypteres are well developed, large, and frequently conceal the halteres; the transverse suture of the thorax is distinct and prominent. The flies are moderate to large in size. Here belong the houseflies, flesh flies, blowflies, etc.

Section II, *Pupipara:* The Pupipara is a remarkable group of flies. They are all, except Braula, bloodsucking ectoparasites of mammals and birds. Their structure has been greatly modified to fit them for their parasitic habits. Their bodies are tough, leathery, and the abdomen is indistinctly segmented; they may be winged or wingless and the mouth parts are fitted for piercing and sucking blood. Larval development takes place within a uterinelike structure of the female (except *Braula*), and the young are deposited as full-grown larvae. Some of the species are of importance as they attack domestic and game animals and act as vectors of disease (the sheep tick or ked, *Melophagus ovinus* and *Trypanosoma melophagium,* the causative agent of sheep trypanosomiasis; *Lynchia maura* and *Haemoproteus columbae* of pigeons).

It is not feasible to prepare a key to all the families of Diptera that affect man. The following table will aid in separating the more important families of Diptera that are of medical importance:

KEY TO THE PRINCIPAL FAMILIES OF DIPTERA (ADULTS) ASSOCIATED WITH HUMAN DISEASE OR KNOWN AS BLOOD SUCKERS

1. Flies of a leathery or horny texture, living in the adult stage as bloodsucking ectoparasites on birds or mammals; they may be winged, wingless, or with vestigial wings; abdomen not distinctly divided into segments; the antennae are short and inserted in small pits, not easily seen. (The group Pupipara) 2

Flies not as described above: abdomen with distinct segments; never external parasites living as adults on birds or mammals; antennae not inserted in pits, usually easily seen; usually with one pair of wings 4

2. Head small, narrow, folded back in a groove in the thorax. Wingless. Parasites of bats .... *Nycteribiidae*

Head not as described above, in normal position 3

3. Palpi elongate, forming a sheath for the piercing mouth parts. Usually

winged with the veins crowded anteriorly. Parasites of birds and mammals .... *Hippoboscidae*

Palpi not forming a distinct sheath for the piercing mouth parts but broad and leaflike. Winged or wingless and in the winged forms the veins evenly distributed. Parasites of bats .... *Streblidae*

4. Antenna consisting of eight or more freely movable, nearly similar segments; anal cell (Fig. 93) widens toward the margin of the wing. The group Nemocera 5

Antenna consisting of not more than four or five well-defined segments; the segment beyond the second may appear as more or less consolidated into rings or annuli 9

5. The costal vein is not continued beyond the apex of the wings; hairs and scales seldom present (Fig. 145) 6

The costal vein surrounds the wing; hairs, often dense, on the wing or scales present on the veins, especially on costa and posterior margins of wing 8

6. Antenna shorter than the thorax, composed of ten or eleven closely united, similar segments; never plumose; legs strong, the hind pair more or less dilated: body thickset; wings broad with few veins. (Black flies) .... *Simuliidae*

Antenna longer than the thorax, usually bushy with long hairs. In general not as described above 7

7. Dorsum of thorax with a longitudinal groove; wings narrow and, in life, held more or less rooflike; mouth parts not fitted for piercing. (None are known to be of medical importance; the gnats) .... *Chironomidae*

Dorsum of thorax without a longitudinal groove; wings held flat and superimposed over each other when at rest; wings often spotted (Fig. 153). Mouth parts fitted for piercing. (Punkies) .... (*Heleidae*) *Ceratopogonidae*

8. Small mothlike flies; mouth parts very short; wings and body clothed with long hairs; wings with long parallel veins; scales on wings absent .... *Psychodidae*

   A. Wings with the second longitudinal vein three-branched, the third branch arising near the base. (Fig. 88). Not known to be of medical importance .... Subfamily *Psychodinae*

   AA. Wings with the second longitudinal vein three-branched, the third branch arising near the middle of wing (Fig. 88). (Of great medical importance) ... Subfamily ***Phlebotominae***

Not mothlike flies; posterior margin of wings and most of the veins with coarse scales (Fig. 93); mouth parts elongate, slender, well adapted for piercing (most species). (The mosquitoes) .... *Culicidae*

9. Antenna consisting of four or five segments, the segment beyond the second may appear as more or less consolidated into rings but can be easily counted (3 to 8 rings); squamae large. (Horseflies) .... *Tabanidae*

Antenna consisting of only three segments 10

10. Last segment of antenna small and ending in an elongate style or arista (Fig. 162). (The snipe flies) .... *Rhagionidae*

Last segment much larger than the others and with a dorsal arista either bare or plumose (Fig. 51 *1*) or a terminal arista 11

11. Wing with stout veins (2 or 3) near the inner costal border; other veins are weak and extend outward to the wing margin; no cross veins .... *Phoridae*

Wing not as described above 12

12. Anal cell elongate reaching nearly to the margin of the wing; a spurious or false vein present between the third and fourth longitudinal veins; usually brightly colored, flower-loving flies (Fig. 211) ...... *Syrphidae*

Anal cell short, truncate (Fig. 172 a); spurious vein absent 13

13. Second antennal segment with a longitudinal cleft or suture on its upper outer edge (Fig. 51 ds); squamae usually conspicuous; thorax generally with a conspicuous transverse suture 14

Second antennal segment without a longitudinal cleft on its upper, outer edge; squamae usually small or very small; thorax usually without a complete transverse suture 18

14. Mouth parts vestigial. (The warble flies and botflies, including Cuterebridae and Hypodermatidae) .... *Oestridae*

Mouth parts well developed and functional 15

15. Hypopleura without a well developed row of bristles below the posterior spiracle (Fig. 85). Small hairs may be present. Arista of antenna usually hairy or plumose. (Houseflies, stable flies, glossina flies) .... *Muscidae* (and *Anthomyiidae*)

Hypopleura with a well-developed row of bristles (Fig. 85) or tuft of bristles 16

16. Postscutellum and postnotum appearing in side view as double convexities (double chin effect under the scutellum). Usually strongly bristled flies. All parasites as larvae, mostly on other insects .... *Tachinidae*

Postscutellum not strongly developed so that only the single convex postnotum appears in side view 17

17. Flies in which the coloration is largely metallic, blues, dark blues, black, or shades of green. A few species are not metallic but have golden hairs on the thorax among the bristles (*Pollenia*); usually four notopleural bristles present. (The blowflies) .... *Calliphoridae*[1]

Flies in which coloration is mainly gray, silvery, intermixed with darker colors; rarely more than two notopleural bristles present. (The flesh flies) .... *Sarcophagidae*[1]

18. Mouth parts vestigial, sunk in a tiny oval pit; large, brownish, fuzzy flies (15 mm. or more). (Horse botflies; Figs. 206–208) *Gasterophilidae*

Mouth parts well developed, not sunk in a pit 19

19. Subcosta vestigial; if present it extends but a short distance beyond the humeral cross vein but does not reach the costa 20

Subcosta present and extending to the costa (but must be looked for with care as it is almost concealed beneath the base of the 1st longitudinal 21

20. Sixth longitudinal and anal veins absent; ocellar triangle large as compared with size of head; subcosta only present at base and appears as a minute fold; costa with only one fracture (Fig. 178). Very small flies (1 to 3 mm.). (Eye gnats) .... *Chloropidae*

Sixth longitudinal vein and usually anal vein present; subcosta more distinct but does not reach the costa; costa with two fractures. (The fruit flies) .... *Drosophilidae*

21. Palpi vestigial. Small, shiny black, brown, or reddish flies with few bristles. Head spherical and abdomen wasp-shaped .... *Sepsidae*

Palpi well developed. Also small flies but not of the shape indicated above. (The cheese skipper) .... *Piophilidae*

A KEY TO THE LARVAE OF SOME OF THE FAMILIES OF DIPTERA MENTIONED IN THE KEY TO THE ADULTS

1. Head well developed, enclosed in a horny capsule, not retractile; mouth parts normal, the mandibles moving laterally in feeding 2

Head not well developed but if partially developed the mandibles move vertically, parallel to each other or obliquely inward; or with no visible head, and the anterior end pointed and provided with mouth hooks or reduced parts (Figs. 159,160,173); or the entire larva grublike, rounded at both ends (Fig. 210); or, possessing an elongated siphon at end of abdomen (Fig. 211) 7

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[1] These two family names are retained here though the grouping of the genera of the Muscidae, Calliphoridae, and Sarcophagidae varies with different specialists. These names are still in common usage in medical literature and include the most important genera affecting man and animals.

2. Aquatic or semiaquatic larvae, living only in swift streams or in tree-holes, mud, edges of ponds, or in open water 3

3. Prolegs lacking on all segments of the body 4

Prolegs present on some segments of the body (Fig. 149) 6

4. Head distinct; thorax and abdominal segments divided secondarily into annuli or rings, usually each ring with a dorsal plate; respiratory openings on prothorax and anal segments (amphipneustic) .... *Psychodinae*

Head distinct; the segments of thorax and abdomen without secondary divisions and otherwise differing from above couplet 5

5. Thoracic segments fused, forming a more or less greatly enlarged portion, distinctly thicker than the abdomen (Fig. 105); respiration by spiracles located at end of elongated tube (siphon) or flattened posterior spiracles (metapneustic). (Mosquitoes, see pp. 250–332) .... *Culicidae*

Thoracic and abdominal segments about equal in diameter, the thoracic segments not greatly enlarged; larvae snakelike (Fig. 152 *C*) with rather smooth bodies. (*Culicoides, Bezzia,* and others; punkies) .... (*Heleidae*) *Ceratopogonidae*

6. Two prolegs on each of abdominal segments 1 and 2; tracheae ending in a pair of discs on eighth abdominal segment .... *Dixidae*

Prolegs (usually only a single one) confined to the prothoracic segment; posterior end of larva with an adhesive disc for attachment. (Larvae confined to more or less swift water; black flies) .... *Simuliidae*

Prolegs present on prothorax and posterior end of body or they may be reduced; never as above. (Gnats) ..... (*Tendipedidae*) *Chironomidae*

Larva with well-developed head and provided with stout bristly hairs or spines (Fig. 90 *b*); body with similar hairs; tip of abdomen with two groups of long hairs; abdomen with prolegs. (Sand flies) .... *Phlebotominae*

7. Larvae cylindrical pointed at both ends; mandibles present, hooklike, and move vertically, parallel to each other; respiratory organs (spiracles) located in a vertical cleft, and usually on the tip of a posterior siphon (Fig. 160) .... *Tabanidae*

Larvae not as described above 8

8. Stout, grublike larvae (aquatic) with a long telescopic terminal siphon.

(Rat-tailed maggots; Fig. 211) .... (in part) *Syrphidae*

Larvae not as described above. For identification of larvæ which do not agree with any of the above descriptions, consult the key given on pages 531–533.

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CHAPTER IX

The Psychodidae: The Moth Flies, Owlet Midges, and Sand Flies

THE members of this family are long-legged, small mothlike flies rarely exceeding 5 mm. in length (Fig. 87). Their bodies and wings are densely clothed with hairs. The wings (Fig. 88) are either oval or lanceolate in shape and, when at rest, are held rooflike or in an arched manner over the abdomen. The venation is simple, consisting mainly of longitudinal veins. The mouth parts are short and not well adapted for piercing (subfamily Psychodinae) or rather long and fitted for bloodsucking (Fig. 89), the

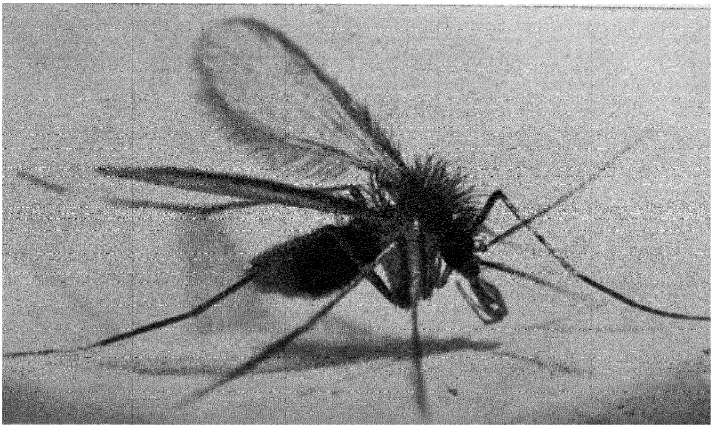

Fig. 87. A sand fly, *Phlebotomus verrucarum.* (From a photograph presented by Hertig.)

subfamily Phlebotominae. The antennae are long, slender, and consist of 12 to 16 segments, each usually with short hairs. The two subfamilies, Psychodinae and Phlebotominae, may be readily separated by the characters given in the key (pp. 228–231).

The majority of known species belong in the subfamily Psychodinae in which the mouth parts are not adapted for bloodsucking. The adults are usually whitish, small, mothlike, and are commonly found about kitchens and outhouses, along creeks filled with decaying wastes, and about sewage disposal plants where they may breed in vast numbers and the adults be very annoying. The larvae occur in decaying vegetable wastes, sewage, dung, exuding sap on trees, fouled streams, and similar situations. None of the species are known to be of medical importance, though their abundance may be annoying at times.

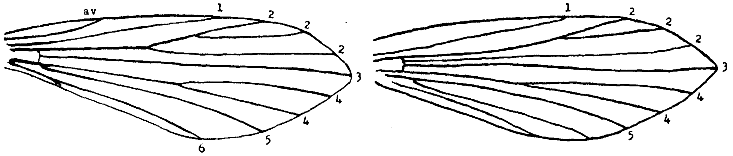

Fig. 88. Left: The wing of a *Phlebotomus* sp. *Right:* The wing of a *Psychoda* sp. The veins and margins of wings are clothed with long hairs but these are omitted. av, auxiliary or subcostal vein. The numbers indicate the longitudinal veins.

✓ In the subfamily Phlebotominae the adults (usually called sandflies) are bloodsucking, the mouth parts being well adapted for piercing (Fig. 89). This group contains but a single genus, *Phlebotomus,* which has been divided into a number of not well defined subgenera. In recent years this family has been studied rather intensively, especially in those areas where pappataci fever, kala azar, leishmaniasis, and Oroya fever occur. Larrouse (1921) recorded 5 species from Europe, 7 from Africa, 7 from Asia, and 12 from the Americas. Sinton (1928) listed 28 species from Asia, and Dyar (1929) reported 21 species from the Americas, only one being found in North America. Barretto (1947) lists over 150 species from the Americas, 6 of which are from North America. Adler (1946) reports 10 species from the island of Cyprus alone. Kirk and Lewis (1946) report 44 species from the Ethiopian region. Yao and Wu (1941) list 13 species from China; Theodor (1948) reports 127 species and 34 varieties from the Old World.

✓DISTRIBUTION: Phlebotomus flies are widely distributed throughout the subtropical and tropical regions of the world. They do not occur very far within the temperate zones, being confined between 40° South and 40° North latitude in the Americas. In Europe and Asia they occur to about 45° North latitude but their southern limit is not known. They are not known to occur in tropical mountain areas above 8000 feet (*P. verrucarum* in Peru). Though widely distributed, the species are usually restricted to more or less definite regions that provide breeding grounds and adequate sources for blood. Their flight range is very limited, scarcely exceeding 100 to 200 yards from their breeding grounds.

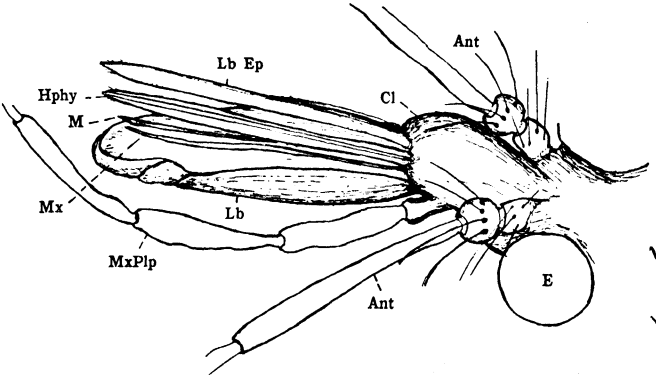

Fig. 89. Mouth parts of *Phlebotomus sergenti* (somewhat diagrammatic). Ant, antennae; Cl, clypeus; E, eye; Hphy, hypopharynx showing the salivary gutter extending throughout its length; Lb, labium; LbEp, labrum-epipharynx; M, mandible; Mx, maxilla; MxPlp, maxillary palpus.

BIONOMICS: The biology, under experimental conditions, of a considerable number of American species (over 25) has been reported during the past ten years. Unfortunately not a single American species has been found breeding under natural conditions though the habitats and activities of the adults of a number of species seem to be well known. The larval habitats of several European and Asiatic species have been discovered in certain areas, but many details of their activities are still lacking. *Phlebotomus papatasii* Scopoli (Fig. 90), the vector of three-day fever or pappataci fever, has been studied extensively in the Mediterranean region and in India. This species is the important vector of pappataci fever throughout its range. It occurs around the Mediterranean region and along the North African area south to the Anglo-Egyptian Sudan east through the former Italian Somaliland to Calcutta and north into Central Asia. The adults are partial to human blood and invade buildings, attacking during the evening and at night. Their bites are severe and the later irritation is almost intolerable to susceptible persons. They are not capable of long flights—only a few yards (50 or more)—but they have been taken in barracks over 25 feet from the ground, and Anderson (1939) reports more cases of fever among soldiers in Peshawar occupying the second story than those on the ground floor. He reports taking the adults 70 feet above the ground level. During the day they hide in holes and cracks of walls, crevices, tree holes, dark rooms, latrines, and any place of darkness and freedom from air currents. The adult life is believed to be comparatively short, probably not over two to three weeks. Under experimental conditions the species is easily reared when the necessary larval food, such as moist soil with adequate decaying animal and plant wastes, is provided. The females require blood meals for the development of the eggs. After the flies mate eggs are laid in small batches, preferably in cracks and crevices of the soil. Several batches are usually laid and blood meals are required between each batch. Anderson (1939) reared this species in 31 days at Peshawar, India, where the temperature ranged from 80° to 84° F. at night to 100° to 107° F. during the day. He fed the larvae on desiccated rabbit feces and earth. During cool weather the larval life is much prolonged, to 60 days or more. Whittingham and Rook (1923) reared this species in Malta from egg to adult in 42 days. There are four larval stages, and hibernation takes place in the fourth larval stage. The main larval habitats were in loose soil, cracks of buildings, embankments, but not in wet soil. Recently Unsworth and

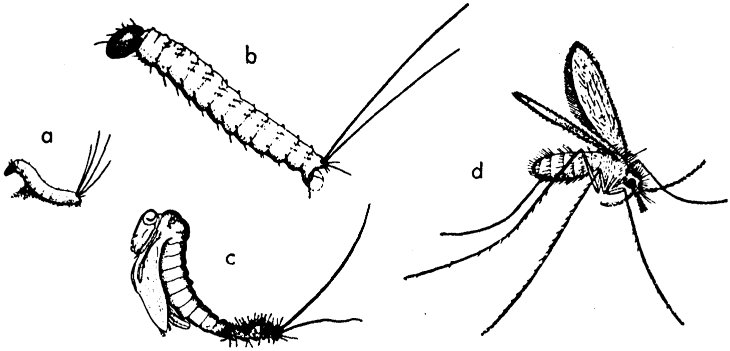

Fig. 90. Phlebotomus papatasii Scop. (*a*) Larva, first instar. (*b*) Sketch of adult larva. (*c*) Pupa with larval skin attached. (*d*) Adult female, resting position. (After Byam and Archibald, *The Practice of Medicine in the Tropics;* from Newstead.)

Gordon (1946) succeeded in establishing and maintaining a colony for experimental work at the University of Liverpool.

Phlebotomus argentipes has been studied in the region of Calcutta, India. It is one of the important vectors of kala azar. Smith *et al.* (1936) report its primary breeding grounds as in the soil within a range of 20 yards of dwellings, cattle sheds, and similar places where there is vegetation and contamination of the ground. The larvae were found mostly in the first three or four inches and localization was frequent. Though this species seems to prefer cattle blood, yet it will attack humans. It is widespread in India east and south of a line drawn from Simla to Bombay (Sinton, 1932). It also occurs in Burma.

Phlebotomus sergenti is widely distributed in the Near and Middle East, in North Africa, Mesopotamia, Iran, and northwest India. It is an important vector of Oriental sore.

In North America six species of *Phlebotomus* are now known. Only one species, *P. diabolicus* Hall, is known to bite man. Very little is known of its biology, though it has been reared in captivity and its life cycle requires 28 to 50 days. The species is known only from southwestern Texas. Its breeding grounds have not been discovered. No species of *Phlebotomus* have been found north of line from Washington, D.C., to San Francisco.

In Mexico and Central America 9 species are listed by Barretto (1946), while in South America over 136 species are recognized by the same author (1947). These species are widely distributed over South America south to Buenos Aires and east of a line drawn from Lima, Peru, to Buenos Aires. No species are recorded from Chile. Only a few of the species can be mentioned here.

Phlebotomus intermedius Lutz and Neiva (= *lutzi*), a vector of mucocutaneous leishmaniasis and of kala azar (experimental), is widely distributed in South America from Venezuela to Argentina, though most records are from Brazil, Paraguay, and Argentina. Bayma (1936), Chagas (1938) and Barretto (1940) have reared this species under experimental conditions. The eggs were obtained from captured females and the larvae reared in earth (rich) usually supplied with animal or decomposing vegetable matter under proper moisture and temperature conditions. At the optimum temperature of 26° to 27° C. the life cycle from egg to adult required 36 days; if the temperatures were lowered to 20° to 22° C. it required 52 or more days. Unfortunately nothing seems to be known about their natural breeding places. The adults are crepuscular and nocturnal in their feeding habits. They are more or less domestic in their habits and readily enter buildings for human or other animal blood.

Phlebotomus verrucarum Townsend is the well-known vector of Oroya fever or verruga peruana. It occurs only in the high mountain canyons in Peru (between 6° and 13° South latitude) especially in the Rimac and Santa Eulalia Valleys at elevations of 800 to nearly 3000 meters. Its distribution outside these valleys is not well known. The adults occur abundantly in certain areas in these valleys, especially in houses and less abundantly in caves, crevices, or other outdoor situations. Though it has been reared many times under experimental conditions, its natural breeding grounds seem to have escaped the most diligent search. The life cycle at temperatures of 23° to 25° C. is completed in 6 to 8 or more weeks. Breeding continues throughout the year, though in cold weather hibernation takes place in the last larval stage (4th instar). The adults are constant invaders of human habitations and prefer human blood, feeding primarily during the evening hours and at night. They also feed on dogs, monkeys, donkeys, and the larger mammals. The other two species usually associated with *P. verrucarum* in these high canyons and valleys are *P. noguchii* Shannon and *P. peruensis* Shannon. According to Hertig (1942), *P. noguchii* rarely enters houses, does not feed on man, and its only known hosts are field mice; *P. peruensis* occurs in caves but also enters houses and feeds on dogs and man.

With the more or less definite proof (confirmed in 1940) that the various human leishmania diseases are transmitted by species of *Phlebotomus,* the study of these insects received great impetus in South America where mucocutaneous and cutaneous leishmaniases (caused by *Leishmania braziliensis* and *L. tropica*) are widely distributed; the more recent discovery of kala azar in Brazil by Chagas (1936) added greatly to the necessity for these studies. The work of Barretto (1940 to 1947) and others led to the recognition of 112 new species in South America since 1936, out of a total of 136 species. In addition, the biology, at least under experimental conditions, of nearly 20 species has been reported when previously only three or four species had been reared. Experimental work on the transmission of these diseases by various species of *Phlebotomus* has greatly increased. At present six species have been incriminated as vectors of *Leishmania braziliensis* experimentally or have been found naturally infected; at least two species have been shown capable of transmitting kala azar under experimental conditions. The importance of *Phlebotomus* species as transmitters of disease is well recognized; this is particularly true in Central and South America and in Mexico.

Unfortunately the study of the species of *Phlebotomus* is so difficult that only specialists in the group are qualified to make identifications of the adults. These are based on the structures of the male genitalia (Fig. 91), of the spermatheca of the females, of the hypopharynx, and of other minute characters. The larvae are distinctive (Fig. 90) but no one has ventured to offer keys to separate even the species that have been reared.

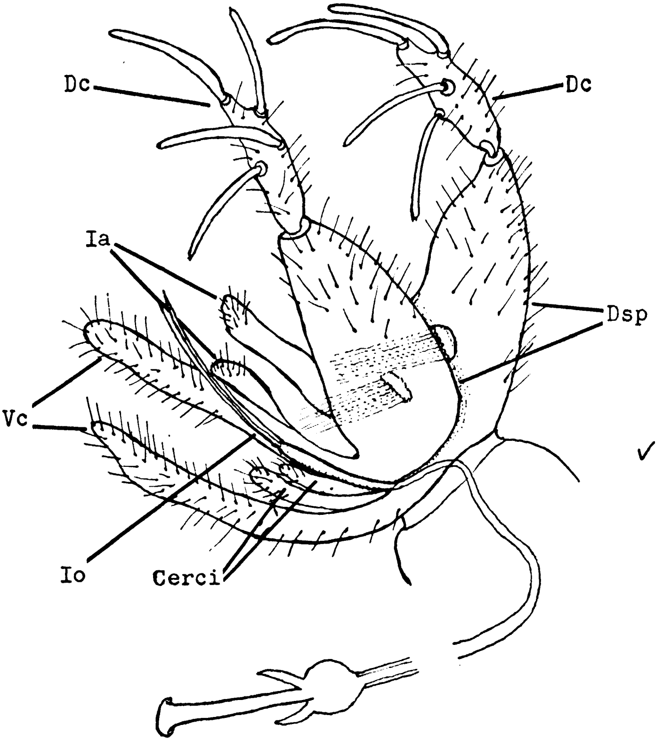

Fig. 91. Male genitalia of *Phlebotomus verrucarum.* Dc, dorsal clasper; Dsp, dorsal side piece; Ia, intermediate appendage; Io, intromittent organ; Vc, ventral clasper.

PHLEBOTOMUS AND DISEASE

PAPPATACI FEVER, THREE-DAY FEVER, OR SAND-FLY FEVER: This disease is endemic throughout the Mediterranean region, India, Ceylon, parts of China, East Africa, and parts of South America. The disease is characterized by sudden onset, fever of 103° to 104° F., which usually falls on the third day, severe headache, and pains. Recovery is usually slow but mortality is nil. The etiological agent is a virus that has not been isolated. It is present in the blood stream 24 hours before the onset of the disease and disappears in from 24 to 48 hours of the disease. Doerr and his associates (1908, 1909) demonstrated that *P. papatasii* could transmit the virus of this disease, and their work has been confirmed by numerous investigators. The fly obtains the virus during its presence in the blood stream of patients suffering from the disease. In the fly there is an incubation period of six to nine days before the fly is capable of transmitting the virus. The incubation period in man is from three to ten days. Whittingham and Rook (1923) demonstrated that infected sand-flies can transmit the virus to their offspring, and Moshkovsky (1937) obtained similar results. Sabin *et al.* (1944) were unable to confirm these results. Though this disease is present in regions where *P. papatasii* is not known to occur, yet no other vector has been discovered or incriminated up to the present time. There is no known animal reservoir except man.

OROYA FEVER, VERRUGA PERUANA, OR CARRION'S DISEASE: Oroya fever and verruga peruana were long regarded as distinct diseases, or different manifestations of the same disease as held by Peruvian physicians. Oroya fever is the severe form of the disease and is characterized by high fever and anemia, often resulting in death. Verruga peruana is the cutaneous form involving verrucous eruptions or nodules, with usually few deaths. The former has been called "Carrion's disease" after Daniel Carrión, a student at Lima, who, on August 27, 1885, infected himself with blood from a verruga nodule and developed Oroya fever from which he died, thus apparently proving that the two diseases were in some manner connected. The disease is restricted to high, narrow, mountainous valleys, principally on the western slopes of the Andes in Peru between 6° and 13° South latitude. It has recently been reported from southern Colombia, Ecuador, and the eastern slopes of the Andes, thus extending the known distribution to 2° North latitude. The disease appears to be restricted to elevations of from 2500 to about 8000 feet in these areas. Practically all persons living in the zones of the disease suffer from the disease and become immune. However, it is very deadly to nonimmunes as demonstrated during 1870 when over 7000 persons died while trying to build a railway from Lima to Oroya. Later epidemics occurred during the construction of bridges and tunnels.

The etiological agent is *Bartonella bacilliformis* Strong *et al.* (1915). This organism occurs in the red blood cells and the reticulo-endothelial cells of the lymphatic system and the viscera. It has been successfully cultured, and infections have been produced in monkeys with these cultures, though apparently only the verruga type; no case of Oroya fever has been produced in monkeys.

TRANSMISSION: Townsend (1913, 1914) was the first to incriminate *Phlebotomus* flies as the vectors and he described *P. verrucarum* as the transmitter in the high valleys of Peru. His experiments, though not absolutely conclusive, demonstrated that his assistant (out of three sleeping in the verruga area) came down with the disease after being bitten by sand flies (55 bites) through accidental exposure of his arms while sleeping under a net. The other two were not bitten. A second case was of a British sailor who permitted himself to be bitten by wild sand flies and who developed what appeared to be the disease, but confirmation of this was apparently never established. "It is most unfortunate that this experiment should have resulted inconclusively for lack of definite diagnosis of the subject's various clinical symptoms, since it is the only recorded human transmission experiment with Phlebotomus" (Hertig, 1942). Townsend's work was not confirmed till Noguchi and his associates (1929) succeeded in transmitting the disease to monkeys by crushed, infected *Phlebotomus verrucarum* sent from Peru to New York by Shannon. Though much experimental work has been done on the transmission of this disease, the results are not very gratifying. Battistini (1929, 1931) succeeded in infecting monkeys both from the bites of wild flies and from the injection of suspensions. Hertig (1942) succeeded in infecting five out of eight monkeys by the bites of wild sand flies taken in the verruga zone in Peru. He also succeeded by using inoculations of cultures of *Bartonella bacilliformis*. In no case did he observe a typical case of Oroya fever but he did demonstrate the presence of the etiological agent in the experimental animals. Hertig's (1942) work has apparently proved that only *P. verrucarum* is the vector in the Peru area as *P. noguchii* does not bite humans and rarely enters houses; *P. peruensis* is usually scarce and is restricted to the upper part of the zone of verruga disease in the Rimac and Eulalia Valleys. Hertig (1942) was unable to find any developmental cycle of the etiological agent in the sand flies, though he found massive infections of the proboscides of both males and females, taken in the wild, with organisms not quite typical of *B. bacilliformis*. What relation these massive infections have in relation to verruga is still undetermined. At the present time only *P. verrucarum* has been definitely incriminated as a vector, yet no direct human infection by the bites of this species has been made. As the disease has been found in areas in Colombia and Ecuador, other species of *Phlebotomus* must be involved. There is no known animal reservoir except man.

As there is no known treatment for either Oroya fever or the verruga stage, it would seem that the use of DDT might prove effective in destroying the adults either by direct spraying or by residual effects. Some of the new repellents might also prove efficient. As their breeding grounds have never been found, nothing can be done in the control of larvae.

KALA AZAR OR VISCERAL LEISHMANIASIS: "Kala-azar is an acute, sub-acute or chronic infectious disease caused by a protozoan parasite, *Leishmania donovani* Ross, 1903 or *L. infantum* Nicolle, 1908, occurring in children and adults, and characterized by splenic and hepatic enlargements, an irregular remittent fever, progressive anaemia, leucopenia, cachexia, and a high mortality" (Archibald, 1921). This disease has a wide distribution around the Mediterranean, is local in the Sudan, Transcaucasia, Turkestan, Kenya, French Equatorial Africa, and Nigeria, and covers an extensive area in northeast India and in China from Canton north to Peking, extending deep into Manchuria with many scattered areas in other parts of China. Recently (1936 and later) it has been found in northeastern Brazil, and the Chaco region of the Argentine, with scattered reports of cases in various other parts of South America. Before the development of the newer treatments with various antimony compounds (1915) the death rate was about 95 per cent of cases (Napier, 1946). Still newer and better treatments have been developed so that the disease is not the terror it was in the days when vast numbers died in epidemic waves, such as swept through Bengal, Assam, and other parts of India. After the discovery of the causal organism intense search followed to determine the method of transmission. It can only be transmitted from the sick to the well by some stage of the parasite *Leishmania donovani,* and this would require some vector as all other means of transmission had been negative. *Phlebotomus* flies were early suspected (Sergents, 1904) as vectors of leishmania and certain species when fed on the blood of kala azar patients showed the same development stages in their intestines as in artificial cultures—the leptomonad stage. Yet despite the development of this flagellate stage and its migration forward to the esophagus, pharynx, and buccal cavity of the experimental flies, all efforts to obtain infection in experimental animals or human volunteers proved failures. However, Shortt *et al.* (1931), Napier *et al.* (1933), and Smith and Murkirjee (1936) reported successful infections of hamsters by the bites of infected *P. argentipes.* These consisted of only three apparently successful transmissions out of a large number of trials. Though numerous experiments were carried out with these flies, it was not till Smith *et al.* (1940) recognized the significance of what are now called "blocked" flies that rapid progress was made in solving the relation of *Phlebotomus* flies to kala azar transmission. They discovered that when flies were fed on infected blood and later fed on plant juices such as that of raisins, the anterior end of the intestine, the esophagus, and the pharynx became so plugged with the developing leptomonad stage that the flies could not successfully obtain a blood meal. They would try to feed again and again but in so doing liberated great numbers of what may be called the infective stage of the parasite into the host. Experiments with "blocked" infected *P. argentipes* by these investigators readily demonstrated the transmission of kala azar to mice and hamsters (1940, 1941). Finally Swanimath *et al.* (1942), using the same technique, successfully transmitted kala azar by "blocked" infected flies to five human volunteers. All bitten by these flies developed the disease within five to eight months. These were the first successful infections of man and the transmission problem seems solved for this species of *Phlebotomus.* Whether this may also prove true for other species suspected of transmitting leishmania diseases remains to be determined.

DERMAL LEISHMANIASIS: The form of the disease that occurs most commonly about the Mediterranean region is dermal leishmaniasis, though the visceral (kala azar) is also present, especially in Greece, Crete, and scattered in all the area. It is mainly a children's disease here, hence the name of the parasite, *Leishmania infantum* (this is now considered identical with *L. donovani*). Dogs in this region are heavily infected and serve principally as the source of human infection. (Apparently dogs have not been found infected in India, though they are known to be infected in North China.)

VECTORS OF KALA AZAR AND DERMAL LEISHMANIASIS: In India the principal vector is *Phlebotomus argentipes* and the distribution of the disease corresponds closely with the known distribution of the fly. In China the accepted vector (though apparently no human infections have been proved by experimental work) is *P. chinensis* and probably *P. sergenti mongolensis;* in the Mediterranean area it is mainly *P. perniciosus,* though in Greece *P. major* is the vector (Malmos, 1947); in the eastern Mediterranean *P. papatasii* is involved, but in North Africa *P. sergenti* is considered important. In the Sudan and other parts of Africa the vectors have not been determined. In South America Chagas (1939, 1940) incriminated *P. intermedius* (= *lutzi*) and *P. longipalpis.* With the known ease with which these flies can be raised under laboratory conditions, it should not be long before experiments with "blocked" flies should give adequate data on the principal vectors throughout the world.

ORIENTAL SORE; ALEPPO, BAGDAD, OR DELHI BOIL; ETC.: This is a cutaneous leishmaniasis caused by *Leishmania tropica.* The disease is widespread about the Mediterranean basin; in Africa south to Angola on the west and to the Sudan and Abyssinia on the east; in Arabia, Mesopotamia, Iran, southern Russia, India, China; and throughout southern Mexico, Central America, and all of South America except Chile. The disease is restricted to the skin, forming ulcers, and a single infection is said to confer immunity. Transmission may be by direct contact with the ulcers. In some countries children are inoculated in those parts of the body where the healed scar will not be observed. However the main agents in the transmission of *L. tropica* are *Phlebotomus* flies. Adler and Ber (1941) report successful transmission of *L. tropica* by *P. papatasii* in Palestine. They obtained 28 lesions from the bites of 26 infected sand flies. In India *P. papatasii* and *P. sergenti* are considered the vectors; in Italy *P. macedonicum* is reported as a vector; in North Africa *P. sergenti* probably is the vector; in the Americas no definite species have been incriminated.

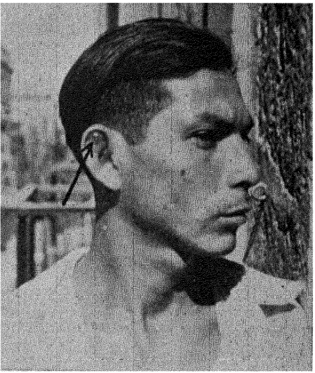

Fig. 92. Photograph of worker with *Leishmania* lesion developing in ear. (Arrow points to lesion.)

Mucocutaneous leishmaniasis or espundia is an ulcerating infection of the skin that may also involve the margins of the nose and the mucosa of the mouth. It is caused by *Leishmania brasiliensis*. The disease is widespread in South and Central America and as far north as Yucatan. In many rural areas as in Minas Geraes in Brazil and in Yucatan among the chicle workers (Fig. 92) this is a serious disease. The transmitters are species of *Phlebotomus* and the following have been incriminated in South America: *P. arthuri* (?), *P. fischeri* (Pessôa and Coutinho, 1941), *P. intermedius* (Aragão, 1922, 1927), *P. migonei* (Pessôa and Coutinho, 1941, and others), *P. pessoai* (Pessôa and Coutinho, 1940, 1941), and *P. whitmani* (Pessôa and Coutinho, 1941).

RESERVOIRS

In the Mediterranean region dogs are probably the chief reservoir of kala azar though cats play a part; dogs are also known to be naturally infected in China, but not in India. Experimentally many animals are readily infected as guinea pigs, rabbits, gerboas, gerbils, hamsters, jackals, dogs, and monkeys. The reservoirs of *L. tropica* and *L. brasiliensis* are probably man though certain species of monkeys, dogs, cats, rats, mice, guinea pigs, and others can be experimentally infected.

CONTROL OF SAND FLIES

So little is known about the breeding grounds of sand flies that it would be impossible to indicate any measures that might be of value in reducing the abundance of flies. In the case of *P. papatasii* proper building measures to reduce cracks, crevices, etc., in walls might be of some aid. *P. sergenti* might be reduced by avoidance of contaminating the ground about homes with animal or vegetable wastes. Nothing is known about the breeding grounds of the other species. The adults might be adequately controlled by the proper use of DDT sprays in buildings, cracks, crevices, or known places where the adults rest during the day. If applied in sufficient quantities the residual effect might be lasting. Hertig and Fairchild (1948) demonstrated the effectiveness of 5 per cent DDT (by weight) in kerosene in Peru during the years 1945–1947. House spraying and spraying of stone walls, resting caves, shelters of all kinds, and suspected breeding areas gave excellent control and the residual effect was very lasting (12 to 19 months on stone walls). This treatment to be most effective should be applied to all buildings, all shelters, stone walls, caves, and other places where sand flies rest since the above authors found that untreated areas only 75 to 100 yards distant were still swarming with the flies. This method of control should be very effective for sand flies in many parts of the world owing to their resting and flight habits. Furthermore, their long larval cycle would prevent rapid multiplication and thus reduce the number of treatments. In addition to controlling the sand flies, other insects as mosquitoes and houseflies would be greatly reduced.

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CHAPTER X

Mosquitoes: Their Structure, Biology, and Classification

THE Culicidae or mosquitoes are easily recognized by their characteristic wing venation and the presence of a fringe of scales on the posterior margin of the wing and on the veins (Fig. 93). They are slender, soft-textured flies with long antennae (Fig. 95). The segments of the antennae bear whorls of hairs; in most of the males the whorls of hairs are so dense as to give the antennae a bushy appearance (Fig. 96). The family is divided into two subfamilies: the Chaoborinae in which the mouth parts are short and not adapted for piercing; and the Culicinae in which the mouth parts are, in most species, fitted for piercing and sucking blood. Not all the species of the Culicinae take blood; the males do not take blood.

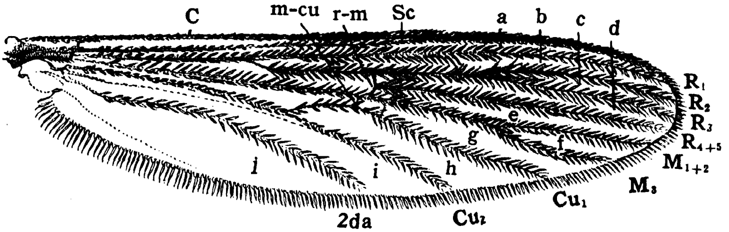

Fig. 93. Wing of *Anopheles walkeri* labeled according to the Comstock-Needham terminology, with the usual terms employed by dipterists in parentheses. The veins: C, costal; Sc, subcostal (*auxiliary*); R_1 (*1st longitudinal*): R_2 and R_3 (*2nd longitudinal*); R_{4+5} (*3rd longitudinal*); M_{1+2} (*4th longitudinal*); $Cu_1 + Cu_2$ (*5th longitudinal*); 2da (*6th longitudinal*); r-m, radio-medial cross-vein (*anterior cross-vein*); m-cu, medio-cubital cross-vein (*posterior cross-vein*). The cells: *a,* Sc (*subcostal*); *b,* R_1 (*1st marginal*); *c,* R_2 (*2nd marginal*); *d,* R_3 (*submarginal*); *e,* R_5 (*1st posterior*); f, M_2 (*2nd posterior*); *g,* M_3 (*3rd posterior*); *h,* Cu_1 (*4th posterior*); *i,* 1stA (*anal cell*); *j,* 2ndA (*axillary cell*). (After Matheson.)

The larvae of the Culicidae are all aquatic. In the Chaoborinae the larvae are predaceous, the antennae being modified for grasping organs (Fig. 94).[1] In the Culicinae the antennae are not so modified and food is obtained by the action of the mouth brushes (Fig. 107). The thorax consists of three fused segments, always wider than the abdomen. The abdomen consists of nine segments and is without appendages. The eighth segment bears a pair of spiracles, either at the end of a long tube, the siphon (Fig. 105) or the siphon may be absent (Fig. 106). The pupae of the Culicinae are all aquatic, active, comma-shaped. The anterior portion (cephalothorax) is enlarged and provided with a pair of horns or trumpets, the respiratory organs (Fig. 103). The abdomen consists of eight segments (nine or ten are recognized), the eighth segment bears a pair of paddles and each paddle has a midrib.

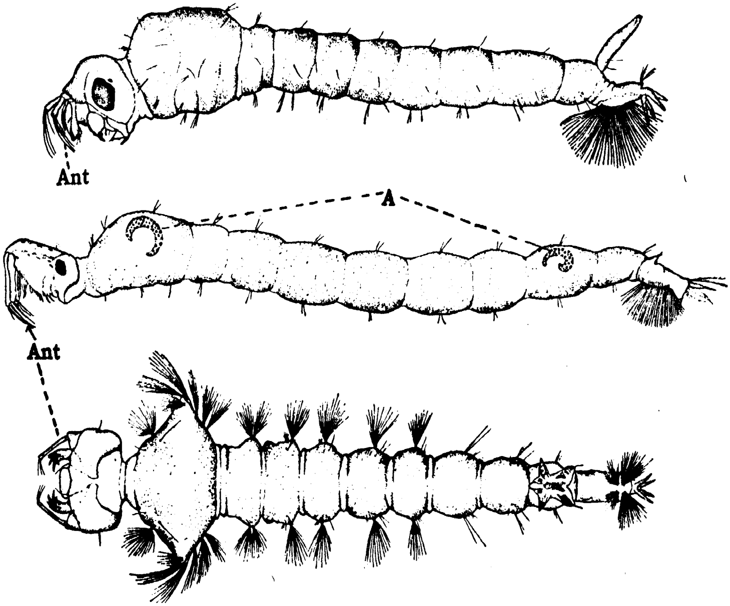

Fig. 94. Larva of Chaoborinae. *Upper:* Larva of *Mochlonyx cinctipes. Center: Chaoborus punctipennis. Lower: Eucorethra underwoodi.* A, air sac; Ant, prehensile antennae.

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[1] The Chaoborinae are not further treated here.

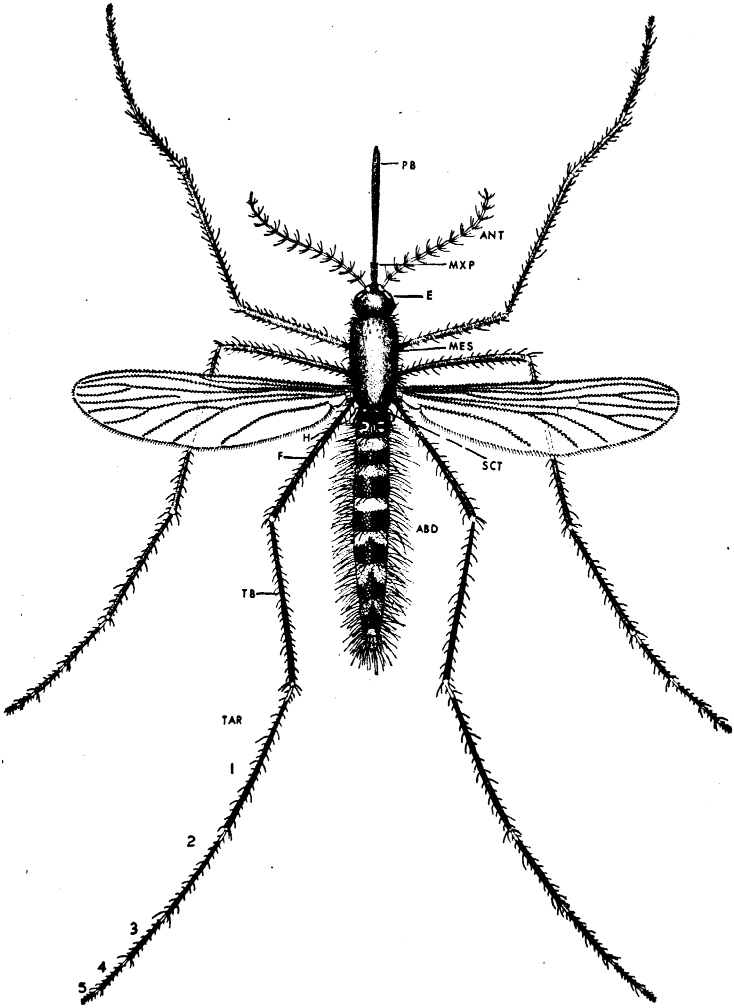
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Fig. 95. Aedes vexans, female. ABD, abdomen; ANT, antenna; E, eye; F, femur; H, haltere; MES, mesonotum; MXP, maxillary palpus; PB, proboscis; SCT, scutellum; TB, tibia; TAR, tarsus with its five segments.

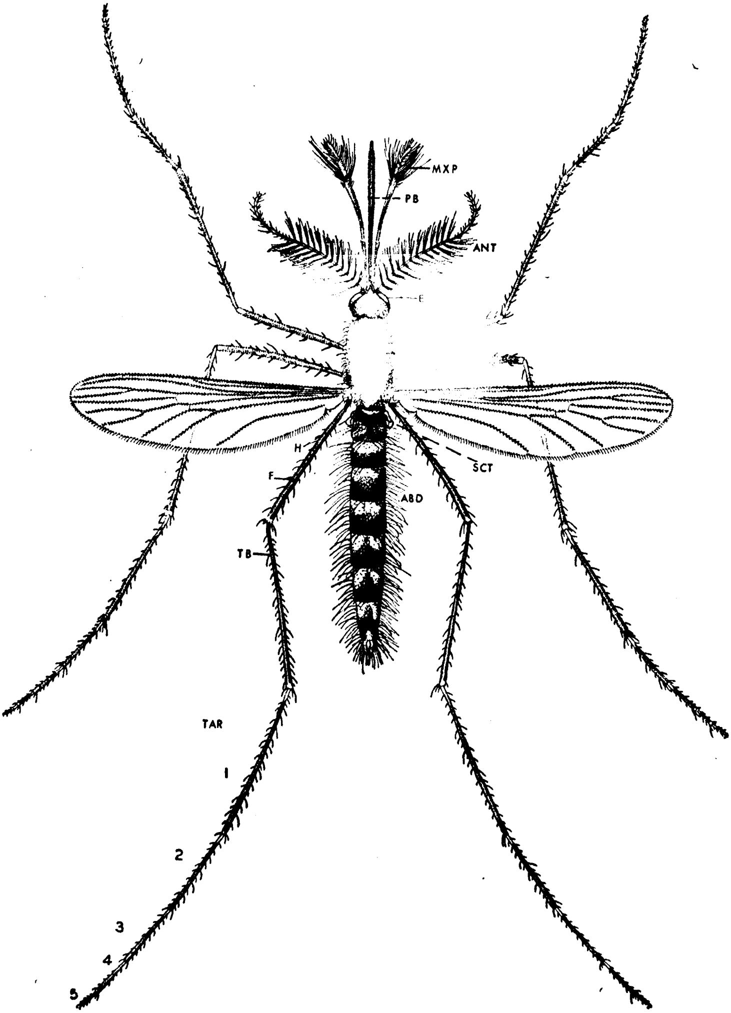
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Fig. 96. Aedes vexans, male. Lettering as in *Fig. 95.*

THE STRUCTURE OF MOSQUITOES

THE ADULT

The more general features of an adult mosquito are shown in figures 95,96. The head is nearly globose and is borne on a slender neck. The compound eyes are prominent, large, and occupy most of the lateral areas of the head; the ocelli are lacking. The small median area between the eyes is called the vertex while the broader portion back of the vertex is generally known as the occiput. The front or frons lies in front of the vertex and bears the antennae. Anterior to the frons and separated from it by a suture is the clypeus, a short, usually nude, snoutlike projection (Fig. 97 Clp). The antennae arise on the sides of the frons between the eyes. Each antenna consists of 15 segments. The first, the scape, is very small and hidden beneath the large, globular second segment, the torus. The remaining segments (13) are filamentous and form the flagellum. Each segment, except the first, of the flagellum has a basal whorl of hairs, which are usually long and bushy in the males (Fig. 96) and shorter and sparser in the females (Fig. 95).

THE MOUTH PARTS: In the female the mouth parts (Fig. 97) consist of an elongated proboscis within which lie the piercing stylets. The proboscis is the labium (Lb), a hollow cylindrical tube, narrowly open along its dorsal face and terminating in two pointed lobes, the labellae. The stylets within the labium consist of (1) the labrum,[2] a long, sclerotized, sharply pointed rod that is grooved on its ventral surface; in cross section it appears U-shaped, the opening of the U closed by a delicate membrane (Fig. 97); (2) the mandibles (md), a pair of delicate, linear-lanceolate structures lying close beside and behind the labrum; (3) the hypopharynx (Hphy), a thin lanceolate structure that is more or less closely applied to the thin mandibles and labrum; (4) the maxillae (Mx), a pair of thin, sclerotized shafts, each terminating in a somewhat enlarged tip that bears a row of small, retrorse teeth; (5) a pair of 4 to 5-jointed maxillary palpi (MxPlp). The maxillary palpi arise at the anterior margin of the head, just beneath the clypeus. The palpi differ in the two sexes. In the females (Culicini) the palpi are much shorter than the proboscis; in the males[3] they are usually densely haired and generally longer than the proboscis, with the last two segments angled upward and tapered to a point

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[2] This is often referred to as the labrum-epipharynx, but here we shall use the word labrum to indicate both structures.

[3] In the males of certain genera and in some species of other genera the palpi of both males and females are similar.

(Fig. 125). In the females of the Anophelini the palpi are straight and about as long as the proboscis (except in the genus *Bironella*); in the males the palpi are nearly as long as or longer than the proboscis while the last two segments are stouter, somewhat flattened, bent upward, and rounded at the apex (Fig. 125).

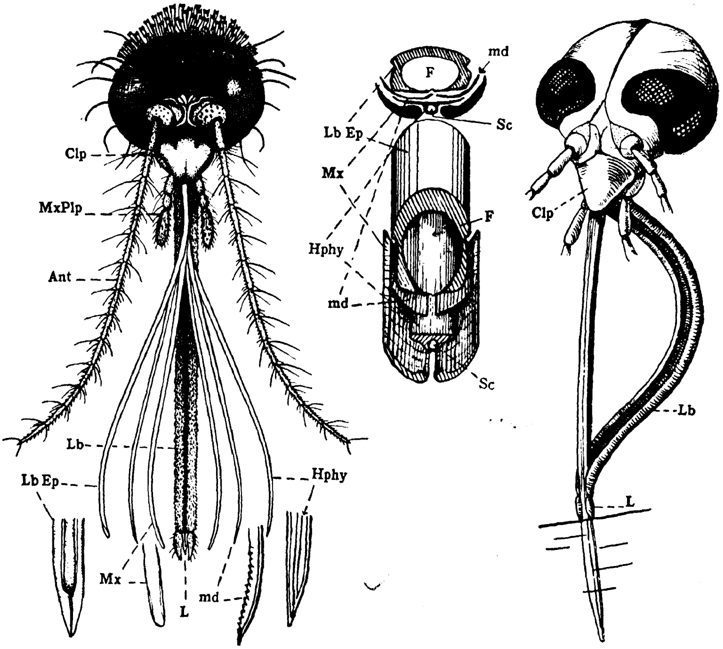

Fig. 97. Mouth parts of female mosquito. *Left:* Frontal view of the head of a mosquito with the mouth parts removed from the labium and the tips of the parts greatly enlarged. *Center:* Cross section and isometric view of the arrangement of the piercing parts. *Right:* A female in the act of taking blood. Ant, antenna; Clp, clypeus; F, food channel; Hphy, hypopharynx; L, labella; Lb, Labium; LbEp, labrum-epipharynx or simply labrum; md, mandible; Mx, maxilla; MxPlp, maxillary palpus; Sc, salivary channel.

The mouth parts of the male are greatly modified. The mandibles, when present, being greatly reduced, and the maxillae being thin and delicate and usually greatly reduced or almost absent.

The action of the mouth parts in taking blood may be observed by allowing a mosquito to bite. When a satisfactory site is selected, the labellae are pressed close to the skin. By muscular action and pressure the cutting mouth parts are forced through the skin and soon all the mouth parts except the labium are deeply embedded; the basal half of the labium is bent back exposing the other mouth parts, and blood can be seen streaming up the food channel; the apical part of the labium still holds the piercing parts in the groove and undoubtedly steadies them.

THE THORAX: The thorax is distinctly wedge-shaped, the base uppermost. The sides of the wedge form the pleura and the apex bears the legs. It is composed of three segments, the second and third being solidly fused together. The spiracles appear as prominent black-rimmed apertures on segments two and three. The prothorax (1st segment) is normally greatly reduced and consists of the two lobes located just back of the head (these lobes are usually widely separated when viewed from the dorsum), the postpronotum (Fig. 98 PPn) and the proepisternum (propleurum). The prosternum lies between the first pair of coxae. The second and third thoracic segments are solidly fused together as in most Diptera. The dorsal surface is composed almost entirely of the large mesonotum and scutellum (dorsum of the second thoracic segment); back of the scutellum is the small, usually smooth postnotum (Fig. 98 9). The sides of meso- and metathorax are divided into several sclerites. The names and position of these sclerites are fully explained in Figs. 98 and 99. On these sclerites are certain setae or bristles that have been assigned definite names. They are of much importance and form landmarks for the placing of many of our species in their respective genera. These groups are as follows (Figs. 98,99): (1) pronotal group (Pn), a varying number of setae massed on the pronotal lobes; (2) proepisternal or propleural group (Ps), a single stout seta or a mass of them on the proepisternum; (3) postpronotal group (PPn), one or several setae arranged more or less in a row just in front of the ridge on the posterior margin of the postpronotum; (4) spiracular group (Sp), a row of setae just in front of the anterior spiracle and behind the postpronotal ridge; (5) postspiracular group (P Sp), a number of setae located on the upper portion of the mesanepisternum and directly behind the anterior spiracle; (6) prealar group (Pa), a small group on the dorsoposterior projection of the sternopleuron; (7) sternopleural group (St P), a group consisting of a variable number of setae located near the posterior margin of the sternopleuron and often crossing it (the location of these setae varies); (8) upper mesepimeral group (UMe), a group located on the upper portion of the mesepimeron; and (9) lower mesepimeral group (LMe), one to several setae on the lower portion of the mesepimeron.

The dorsal area of the thorax offers comparatively few characters of value in systematic work except coloration patterns and the arrangement of setae

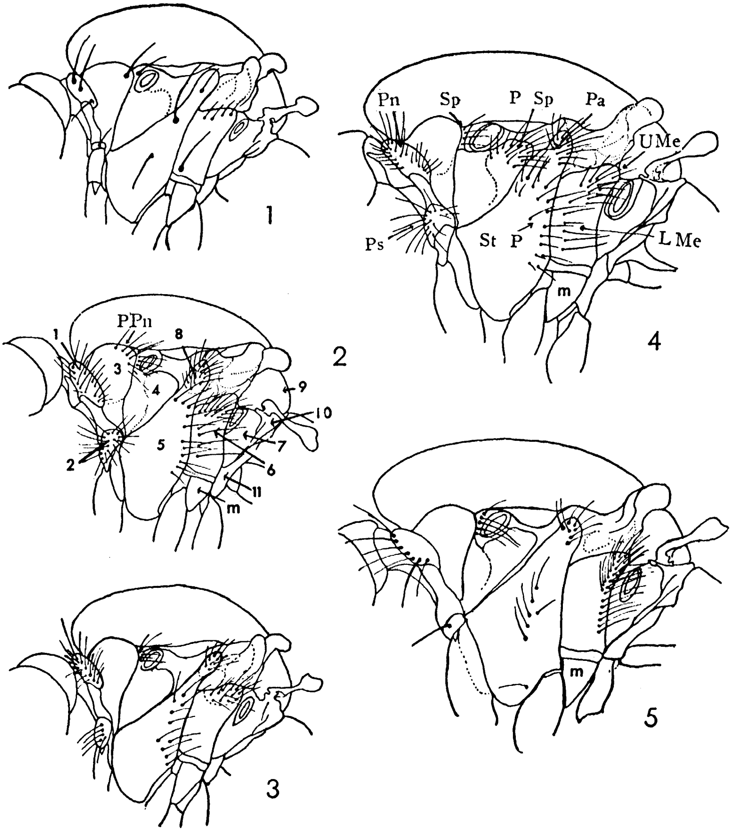

Fig. 98. Lateral views of the thorax of mosquitoes. (*1*) *Uranotaenia lowii.* (*2*) *Culiseta morsitans.* (*3*) *Anopheles punctipennis.* (*4*) *Psorophora ciliata.* (*5*) *Megarhinus septentrionalis.* The sclerites of the thorax (*2*): 1, pronotum (prothoracic lobe); 2, proepisternum; 3, postpronotum; 4, mesanepisternum; 5, sternopleuron; 6, mesepimeron; 7, metepisternum; 8, prealar area; 9, postnotum; 10, metepimeron; 11, meteusternum; m, meron. The setae (*4*): LMe, lower mesepimeral; Pa, prealar; Pn, pronotal; PPn, posterior pronotal or postpronotal; Ps, proepisternal; P Sp, postspiracular; Sp, spiracular; St P, sternopleural; UMe, upper mesepimeral. The dorsal portion extending from 1 to 9 represents the mesonotum (*2*).

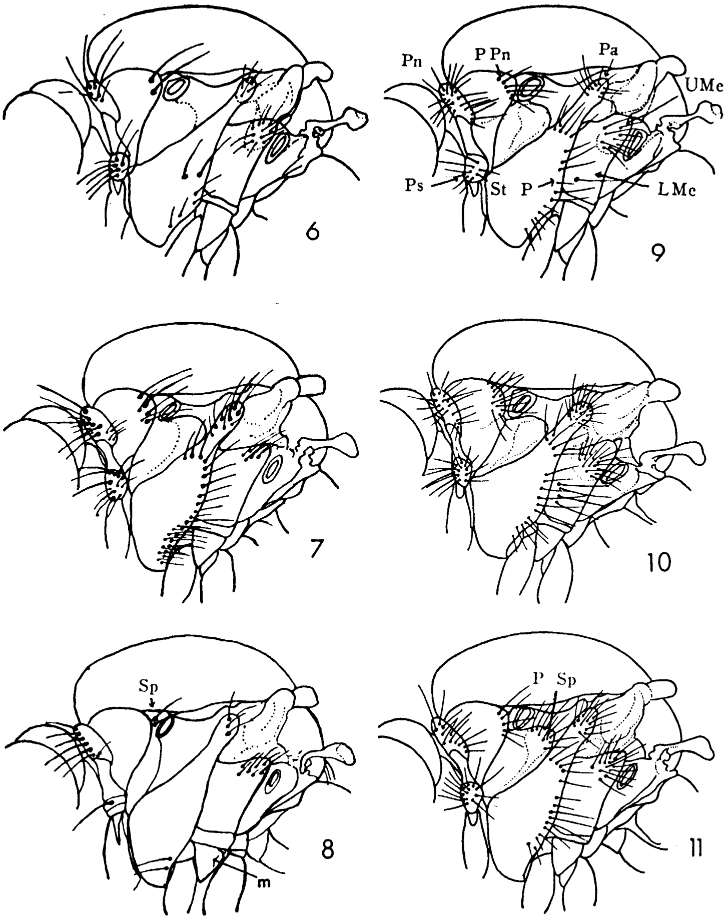

Fig. 99. Lateral views of the thorax of mosquitoes. (*6*) *Orthopodomyia signifera.* (*7*) *Deinocerites pseudes.* (*8*) *Wyeomyia smithii.* (*9*) *Culex pipiens.* (*10*) *Mansonia perturbans.* (*11*) *Aedes vexans.* Explanations as in *Fig. 98.*

and scales. The scutellum is separated by a transverse suture from the mesonotum. In all the genera except *Anopheles* and *Megarhinus* the scutellum is trilobed, and each lobe generally bears stiff bristles and usually scales; in the above-named genera the scutellum is arcuate or rounded behind and the bristles arranged evenly on it.

THE WINGS: The wings are long and narrow (Fig. 93). The venation is characteristic and the presence of scales is very distinctive of this family. The scales are frequently of different colors or may be distributed so as to give definite patterns (Fig. 126). The terminology of the wing veins and cells varies. The Comstock-Needham system and that used by most dipterists is illustrated in Fig. 93. As the venational pattern varies very little throughout the family, the form, shape, and color of the scales and their arrangement frequently offer excellent characters in separating species (Fig. 131). The second pair of wings are represented by small knoblike structures, the halteres (Fig. 96 H).

THE LEGS: The legs are long and slender (Fig. 96). Each leg consists of the usual parts, coxa, trochanter, femur, tibia, and a 5-segmented tarsus. The coxa is short, stout, and connects with the ventral portion of the thorax. The trochanter is a small, short segment connecting the coxa to the long femur. The tibia is slender and about as long as the femur. The tarsus is usually very long and the segments vary in length, though the first one is much the longest. The last segment bears a pair of claws or ungues. The claws vary greatly in size and those of the hind legs are generally smaller than those of the other legs. In the females the claws are usually simple, that is, they do not bear teeth except in most species of the genera *Aedes, Psorophora, Haemagogus, Armigeres,* and some others. In the males the claws of the first pair of legs (and sometimes also the second pair) are usually toothed, though in anophelines one claw is usually reduced and the other is toothed. In nearly all species there is present a small hairy seta (empodium) between the bases of the claws; in the genus *Culex* there is, in addition, a pair of thin padlike structures (pulvilli) beneath the claws that is diagnostic for this genus.

THE ABDOMEN: The abdomen is narrowly elongate, nearly cylindrical, and consists of ten segments, the first eight of which are distinct. Each segment is composed of a tergite that extends down the sides and is connected with the sternite by a pleural membrane. The successive segments are joined by thin membranes (intersegmental membranes). In all the culicines both the dorsal and ventral surfaces are usually covered with dense scales; in the anophelines scales are practically absent or present in restricted areas. Six pairs of spiracles are present on the second to seventh segments. In the female the abdomen is pointed, as in *Aedes,* or truncate, as in *Culex.* The ninth segment is reduced, and between it and the eighth lies the opening of the female reproductive organs. The tenth segment is greatly reduced and bears the cerci and anal opening. In the male the terminal abdominal segments are modified for sexual purposes. Shortly after emergence from the pupa (usually within 24 hours) the eighth, ninth, and tenth segments undergo an axial torsion through an arc of 180° so that the dorsal surface becomes ventral and the ventral dorsal. The tip of the abdomen back of the eighth segment is generally called the hypopygium, male genitalia, or, by some, terminalia.

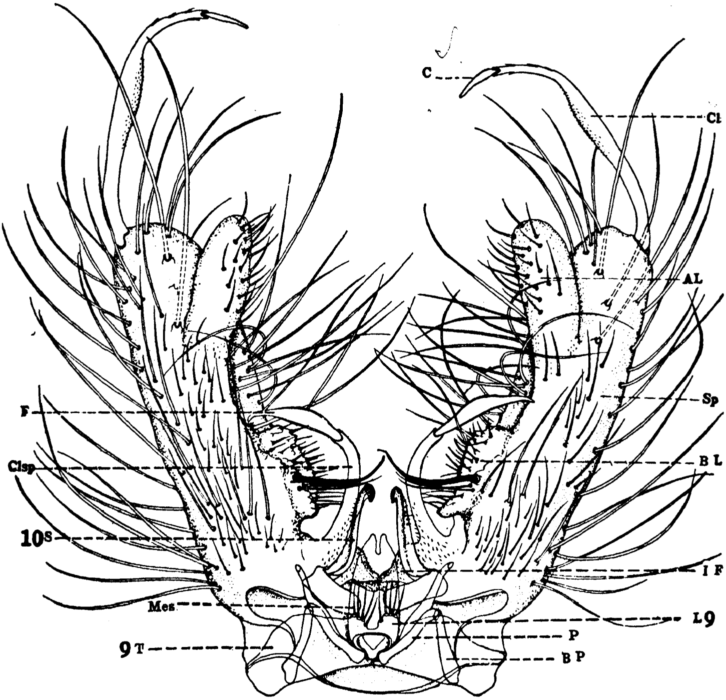

Fig. 100. Male genitalia of *Aedes stimulans.* AL, apical lobe; BL, basal lobe of sidepiece; BP, basal plate; C, claw or spine of clasper; Cl, clasper; Clsp, claspette; F, filament of claspette; IF, interbasal fold; L9, lobe of ninth tergite; Mes, mesosome; P, paramere; Sp, sidepiece; 10S, tenth sternite; 9T, ninth tergite.

MALE GENITALIA: The structure of the male genitalia affords excellent characters for the identification of species and an understanding of these structures is essential. Figs. 100–102 show the main structures to be observed in the genera *Aedes, Culex,* and *Anopheles.*

As the terminal segments (8th to 10th) of the male abdomen undergo an axial torsion of 180°, it is essential to remember that ventral becomes dorsal and dorsal ventral. The terms lower and upper will be used in their ordinary sense but all morphological terms as dorsal, ventral, and names of sclerites will be employed with their correct meaning. Typically the genitalia structures begin with the ninth segment; this segment consists of a complete ring, more or less sclerotized, especially on the dorsal aspect. The tergite (9T, ixT) may possess lobes (L9, T) or the lobes may be greatly reduced or almost absent. From within the ring of the ninth segment arises a pair of large, hollow, forcepslike appendages. The basal parts are stout and are called

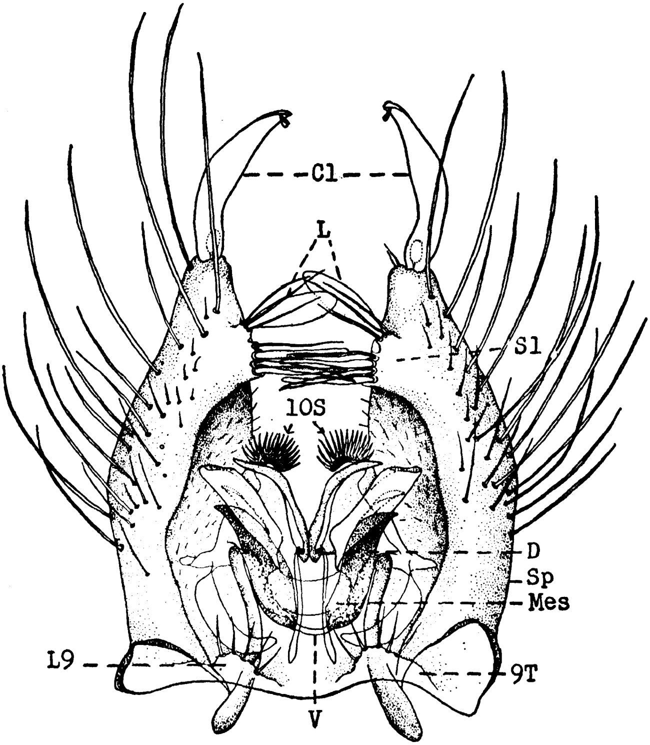

Fig. 101. Male genitalis of *Culex pipiens.* Cl, clasper; D, dorsal bridge; L, leaf of subapical lobe; L9, lobe of ninth tergite; Mes, mesosome; Sl, subapical lobe; Sp, sidepiece; 10S, tenth sternite or paraprocts; 9T, ninth tergite; V, ventral bridge.

sidepieces, or coxites (Sp), or basistyles. The apical appendage of each is long and normally narrow (CL), or it may be expanded (*Psorophora*) or modified into the most bizarre shapes (*Wyeomyia*); it is called the clasper or dististyle. Each sidepiece may bear a basal lobe (Fig. 100 BL) or the lobe may be lacking or the lobe may be replaced by several stout spines (Fig. 102 Ps), parabasal spines. There may be an apical lobe (Fig. 100 AL), the lobe may be subapical in position as in *Culex* (Fig. 101, Sl), or it may be absent. In anophelines there is usually present an internal spine (Fig. 102 IS). Arising from a basal fold that aids in uniting the sidepieces are the claspettes (Clsp); in the Culicini (*Aedes, Psorophora,* etc.; absent in the genus *Culex*) these structures may be very complicated; in the Anophelini they are represented by lobes, the outer or dorsal and inner or ventral lobes (Fig. 102 Dl and Vl). In the median plane, lying directly above and extending beyond the ninth tergite are the sclerotized parts of the tenth segment (10s), the proctiger. The structures here involved have been variously designated and differ greatly in the different genera. The tenth sternite (10s) is usually well developed in such genera as *Aedes, Culex, Culiseta, Psorophora, Mansonia,* and others. In *Anopheles* the tenth sternite is vestigial, only the membranous anal lobe (Fig. 102 Lb) being present. Between the sternites and beneath them or the anal lobe is located the mesosome (Mes) or phallosome, a sclerotized tubelike structure surrounding the penis. It is supported and held in position by the basal plates (Fig. 100 BP) and the parameres (P). The mesosome varies greatly in the different genera and furnishes characters for the differentiation of genera and species. In *Anopheles* the mesosome is a long, slender tube with or without apical leaflets (Fig. 102); in other genera it may assume bizarre shapes as in *Culex* (Fig. 101).

THE PUPA

The pupa is the stage from which the adult emerges. All pupae are aquatic, active, take no food, and are comma-shaped (Fig. 103). The enlarged anterior half contains the future head and thorax of the developing adult. The more slender portion represents the abdomen and is composed of eight segments (nine or ten can be recognized) and a pair of paddles or fins (Fig. 103). Arising from the thorax is a pair of respiratory horns or trumpets, which break through the surface film of the water when the pupa float to the surface and permit air to enter through the spiracles located within the horns.

The abdomen of pupae is provided with various hairs and spines, and these have been studied by various workers in attempts to use them for identification purposes. Though a goodly number of pupae have been figured and described, the number is not sufficiently large to permit us to hope that species

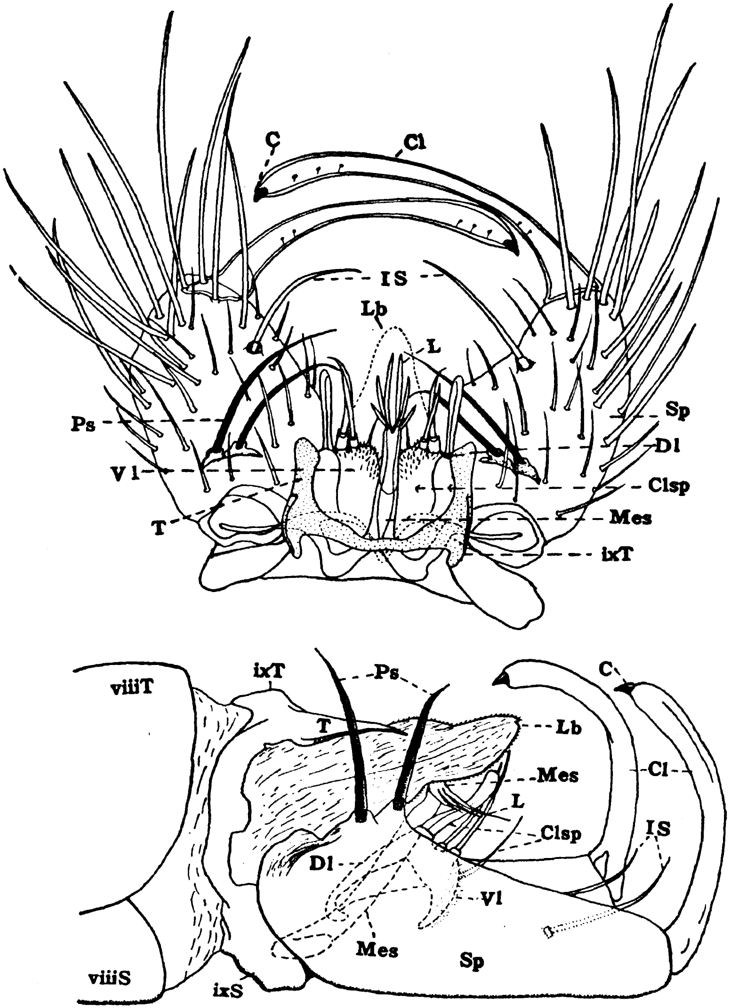
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Fig. 102. Male genitalia of *Anopheles quadrimaculatus*. *Upper:* Lower or dorsal view. *Lower:* Lateral view. C, claw or spine of clasper; Cl, clasper; Clsp, claspettes; Dl, dorsal lobe of claspette; IS, internal spines; L, leaflets of mesosome; Lb, anal lobe; Mes, mesosome or phallosome; Ps, basal or parabasal spines of sidepiece; Sp, sidepiece or coxite; viiiS, ixS, eighth and ninth sternites; T, lobe of ninth tergite; viiiT, ixT, eighth and ninth tergites; Vl, ventral lobe of claspette.

identification by pupae may become well established. The characters most frequently used are the structure of the paddles and the arrangement of the hairs and spines. Anopheline pupae can usually be recognized in that spine A of segments 3 to 7 is stout, peglike, single, and located at the apical angles, while the same spine on segment 8 is in the same position and fringed. In other pupae spine A is usually branched and not located at the exact apical angle (Fig. 104).

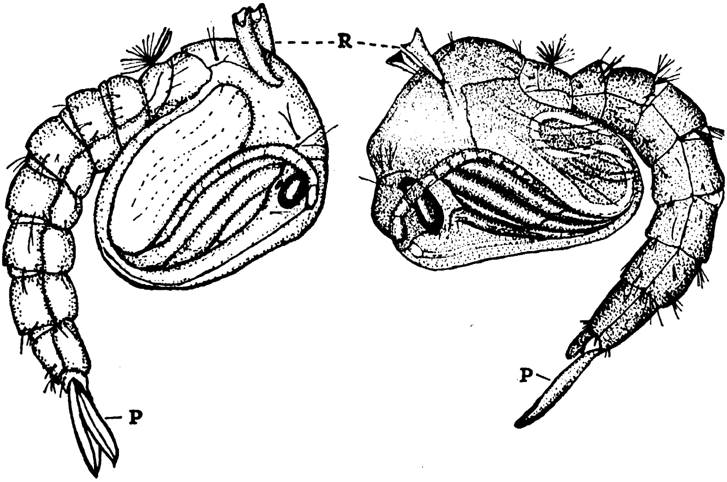
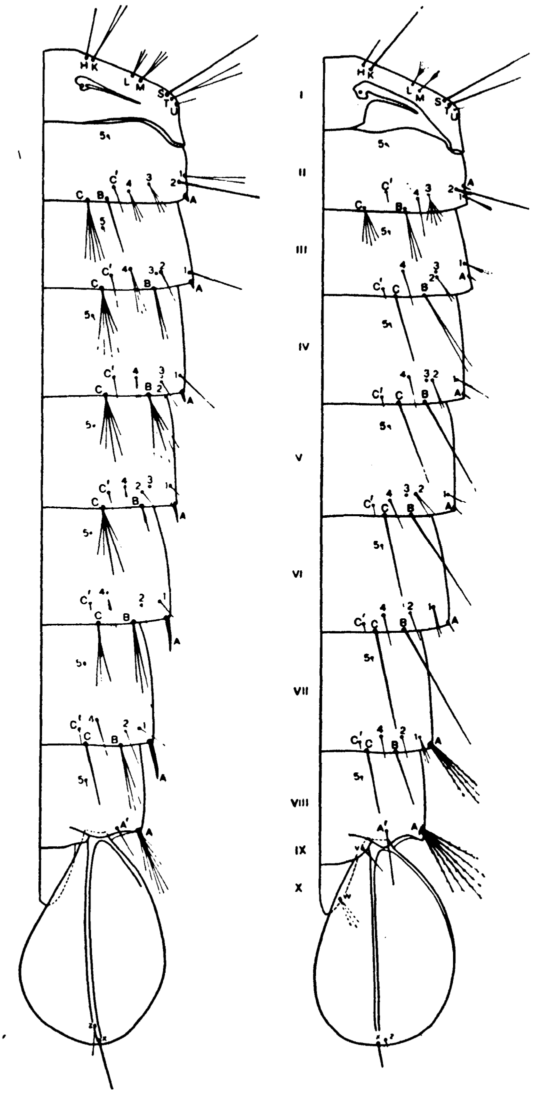


Fig. 103. Pupae of mosquitoes. *Left: Aedes cinereus. Right: Anopheles punctipennis.* P, paddles; R, respiratory horns.

THE LARVA (Fourth instar)

The larvae of all known species are aquatic and their structure adapts them to life in the water (Fig. 113). The larva (Figs. 105,106) is legless and consists of a prominent head, a large, boxlike unsegmented thorax, and a slender abdomen of nine segments.

The head is normally well sclerotized and bears the mouth parts, the antennae, eyes, the remarkable mouth brushes, and an arrangement of hairs or tufts. The mouth parts (Fig. 107) consist of a labrum (often referred to as the preclypeus), a pair of mandibles, a pair of maxillae, and the labium. These are typical mandibulate mouth parts. The mouth brushes are remarkable structures as by their vigorous and rapid movement they direct the food into


H
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3
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1
C
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II
III
IV
V
VI
VII
VIII
IX
X

Fig. 104. Pupal chaetotaxy. *Left:* Typical arrangement of hairs of an anopheline. *Right:* Typical arrangement of hairs of a nonanopheline. The numbers and letters refer to the hairs on each abdominal segment. (After Penn.)

the mouth cavity or serve to capture their prey (some *Psorophora, Megarhinus*). It has been shown by Becker (1938), Cook (1944), and Farnsworth (1947) that the activity of the mouth brushes is due to muscular action and elasticity of the cuticula. Fig. 107 illustrates the muscles and structures involved in this movement. The external and internal messorial muscles (aem, aim) by pulling the palatal bar to a more anterior position depress the mouth brushes. The median palatal muscle (mpa) would then contract and cause the brushes to return to their original position. Hence by the rapid action of these muscles along with the elasticity of the cuticula the mouth brushes are set in active vibration. (Consult Farnsworth, 1947.)

The antenna consists of a single segment and it terminates in a hair and certain terminal spines; in the culicines subterminal spines are present. A tuft of hairs, a single hair, or a branched hair (the antennal hair tuft) is located near the middle of the shaft. The eyes are located on the sides of the head. The large anterior eyes are the developing eyes of the adult and back of them is located the small larval eyes. The various paired hairs on the head are given names, numbers, or letters according to the individual worker. In the culicine and anopheline larvae the principal head hairs are illustrated and named in Figs. 105 and 110.

The thorax bears a large number of hairs and they are so arranged as to indicate the pro-, meso-, and metathoracic segments. The usual numbers applied to these hairs or groups are shown in Figs. 105 and 109. In the anophelines the character of these hair groups is of considerable importance in the identification of species. Many of these have been given names, which are indicated under the illustrations.

The abdomen consists of nine segments. On the dorsal surface of the eighth abdominal segment are the openings of the respiratory system, which, in all the Culicini, consists of a long siphon (Fig. 105 S) through which a pair of tracheal tubes run to the tip; these tracheae can be opened or closed by a series of apical valves which surround the spiracles; in all anophelines the siphon is absent and the spiracles open through a stigmatal plate (Figs. 106,109). The ninth segment is usually more slender, is attached ventroposteriorly to the eighth, and points ventrally and backwards. Its integument is more or less sclerotized forming the dorsal plate or saddle (Fig. 105 DP). This saddle may completely surround (ring) the segment (as in *Psorophora,* some *Aedes*) or be open along its ventral median face. Beyond the saddle the segment appears fleshy and bears at its tip the anal opening and four (rarely two) thin, tapering appendages, the tracheal or anal gills. In addition, the ninth segment bears two important structures, the dorsal brush, consisting of two sets of longer or

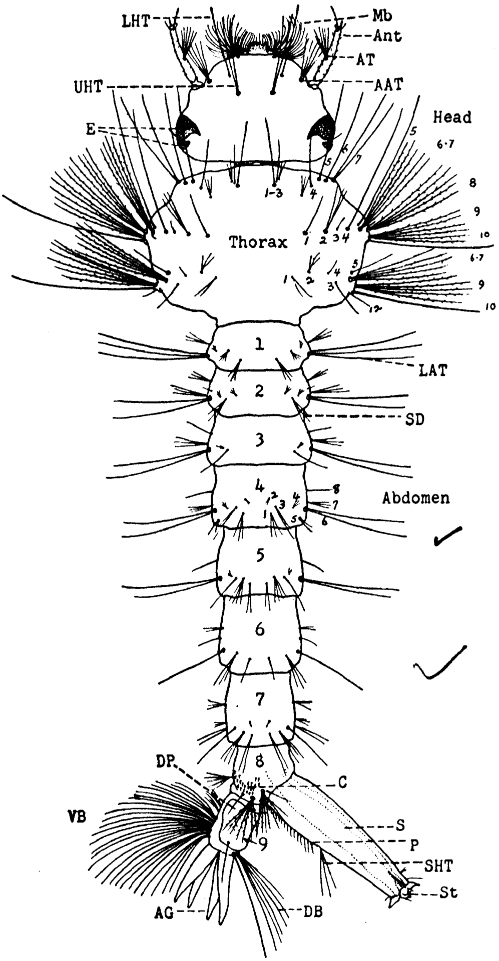
LHT
Mb
Ant
AT
UHT
AAT
E
Head
5
6·7
7
8
9
10
1-3
4
Thorax
1 2 3 4
5
6·7
9
10
12
1
2
3
4
5
LAT
SD
Abdomen
8
7
6
6
7
DP
8
C
VB
9
S
P
SHT
St
AG
DB

Fig. 105. Dorsal view of larva of *Aedes stimulans.* The eighth and ninth segments and the siphon are turned lateral so as to give a side view of them. AAT, anteantennal hair tuft; AG, anal gills; Ant, antenna; AT, antennal tuft; C, comb; DB, dorsal brush; DP, dorsal plate or saddle; E, eyes; LAT, lateral abdominal tufts; LHT, lower head tuft or hair; Mb, mouth brushes; P, pecten; S, siphon or air tube; SD, subdorsal hair tufts of the abdomen; SHT, siphonal or air tube tuft; St, stigma; UHT, upper head tuft or hair; VB, ventral brush; 1–9, segments of abdomen. The small numbers on thorax and segment 4 of abdomen indicate the arrangement of the setae.

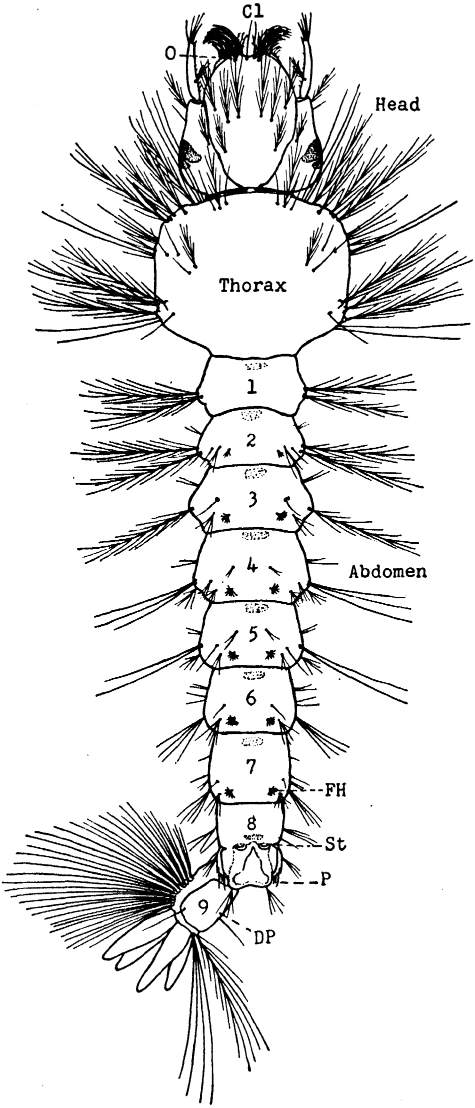
Cl
O
Head
Thorax
1
2
3
4
Abdomen
5
6
7
FH
8
St
P
9
DP

Fig. 106. Larva of *Anopheles punctipennis.* Cl, inner clypeal hairs; DP, dorsal plate; FH, float hairs or palmate tufts; O, outer clypeal hairs; P, pecten; St, stigma of spiracle.

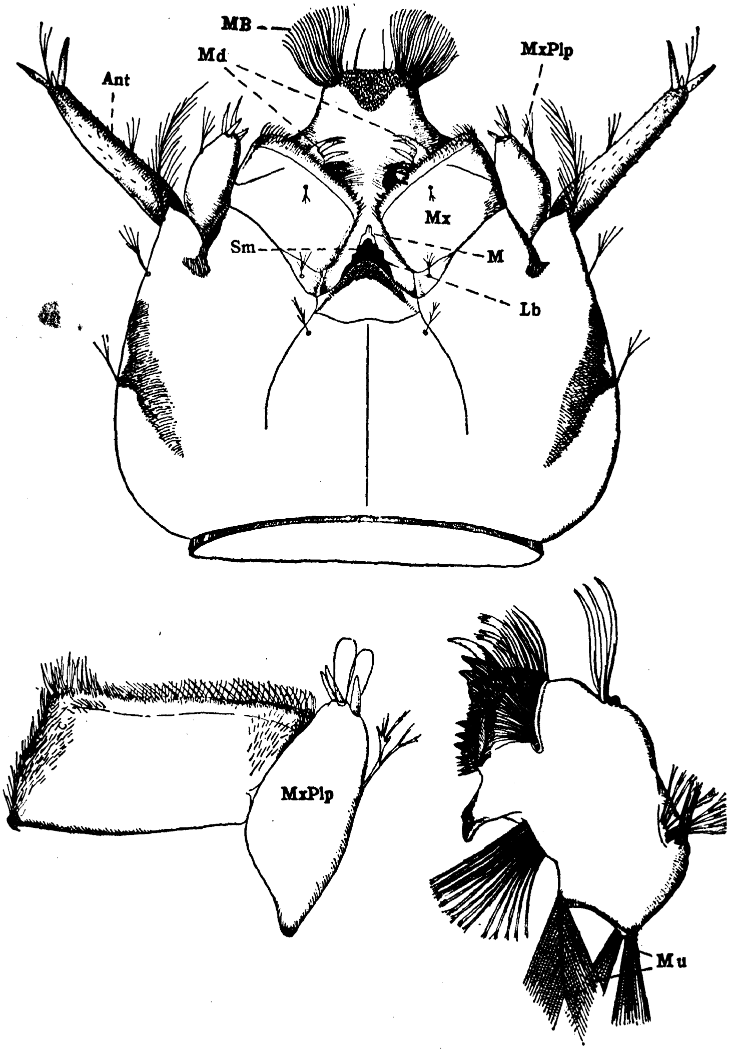
MB
Md
MxPlp
Ant
Mx
Sm
M
Lb
MxPlp
Mu

Fig. 107. Mouth parts of a mosquito larva (*Anopheles*). *Upper:* Ventral view of head. *Lower left:* A single mandible. *Lower right:* A maxilla. Ant, antenna; Lb, labium; M, mentum; MB, mouth brushes (see *Fig. 108*); Md, mandible; Mu, muscles of mandible; Mx, maxilla; MxPlp, maxillary palpus; Sm, submentum.

shorter hair tufts (Fig. 105 DB, only one set is shown; the other is on the opposite side) located at the posterodorsal angle; and, in most mosquito larvae, a ventral brush, consisting of unpaired hair tufts extending from the ventro-apical edge to a greater or less distance forward; the distal tufts usually have sclerotized bases forming a sort of grid or barred area. In the culicines the siphon or air tube has one to several pairs of subventral hair tufts or a median row of hair tufts and, usually on the basal half, a paired row of short, spine-like teeth, the pecten (Fig. 105 P). In some genera the pecten may be absent.

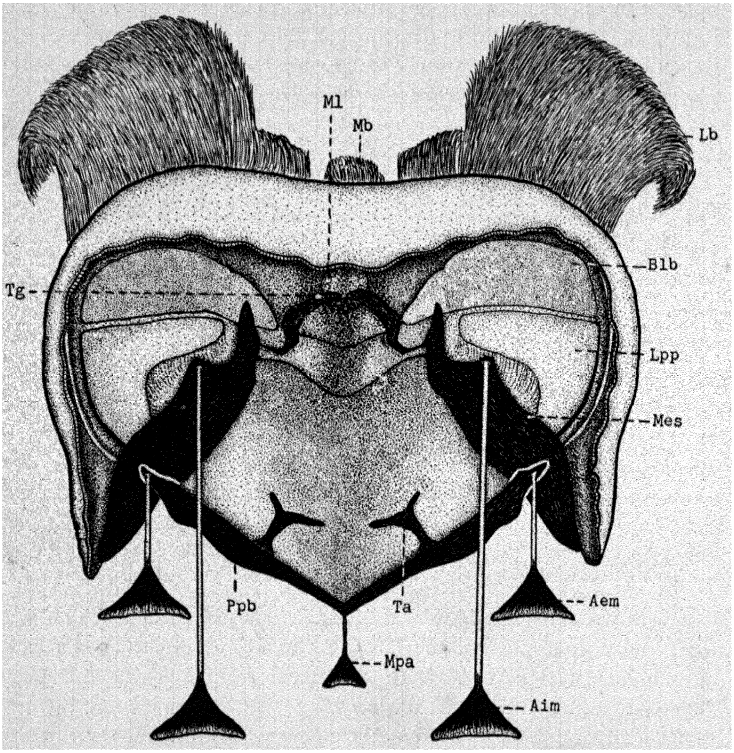

Fig. 108. Internal view looking down toward the mouth brushes to show the attachments that move the brushes. Aem, tendon attaching the external messorial muscle; Aim, same for the internal messorial muscle; Blb, base of brush; Lb, larval mouth brush; Lpp, lateral palatal plate; Mb, median bristles; Mes, messor; Ml, median lobe; Mpa, median palatal muscle; Ppb, posterior palatal bar; Ta, sclerite; Tg, transverse girdle. (After Farnsworth.)

In all anophelines each side of the stigmatal structure has a sclerotized plate that bears a distal row of spines of varying length—the pecten (Fig. 109) or, as it is sometimes called, the comb. The true comb is borne laterally on the eighth segment (Fig. 105 C) and is found in anophelines only in the first-stage larva. The comb consists of a patch of scales arranged in various ways. Each scale may be toothlike, fringed with spinules or with stout branches, and arise independently or be attached to a sclerotized plate.

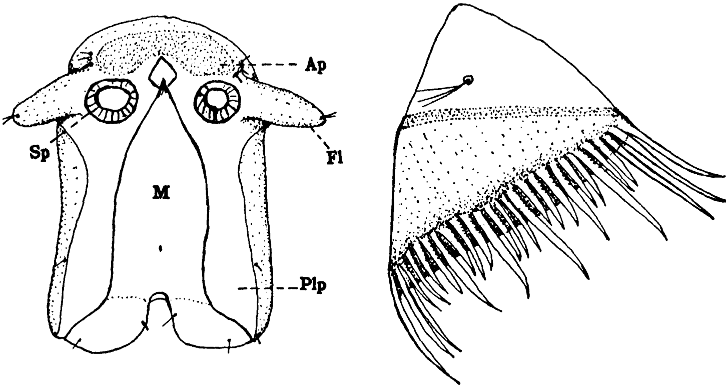

Fig. 109. Left: Dorsal view of spiracle of larva of *Anopheles. Right:* Pecten of larva of *Anopheles.* Ap, anterior plate or flap; Fl, lateral flap or ear; M, dorsal plate; Plp, posterior spiracle plate; Sp, spiracle.

In recent years the chaetotaxy or arrangement of hairs and spines on the thorax and abdomen of mosquito larvae has been closely studied, and names or numbers or both have been assigned to them. Fig. 110 presents the numbering system as interpreted by Hurlbut (1938) for anophelines, and Fig. 105 shows similar numbers assigned by the author to culicines. However, there is great variation among workers and usually each author explains his system.

THE EGG

The eggs (Fig. 111) of mosquitoes are rather characteristic and well protected by several layers—the thin vitelline membrane which surrounds the yolk (the chorion, exo- and endochorion) and a heavily sclerotized outer shell which externally is frequently patterned with small bosses or reticulations (Fig. 112). At the anterior pole is the micropyle, a minute opening for the entrance of the sperm; the micropyle is usually surrounded by a ring of small bosses forming a kind of rosette. The eggs of culicines are generally elongate

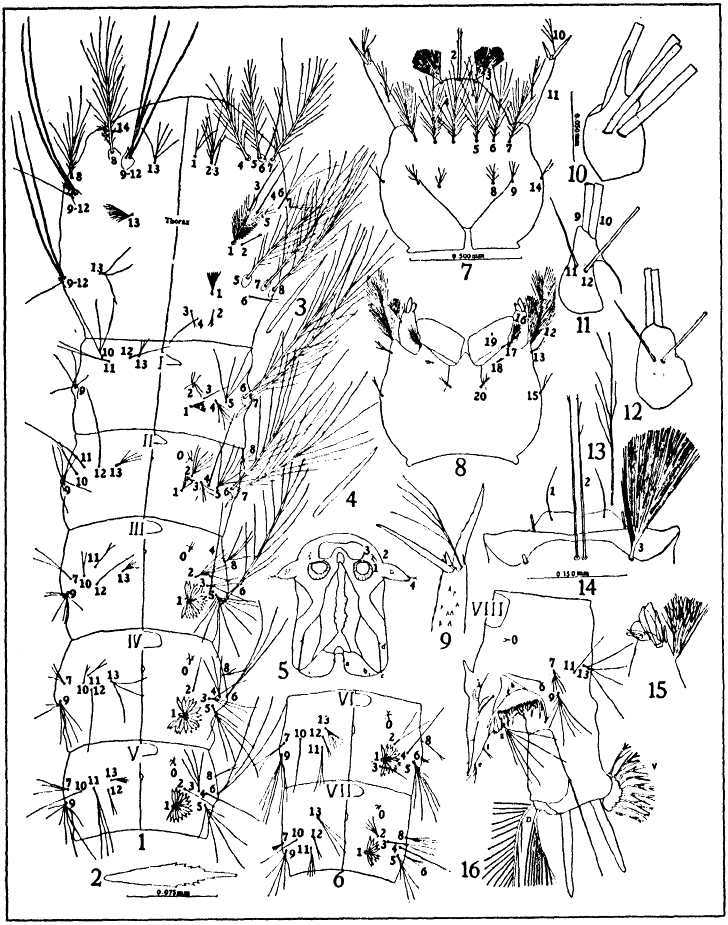

Fig. 110. The chaetotaxy of the fourth instar larva of *Anopheles walkeri;* the hairs are all numbered 1 to 14. (*1*) Thorax and first five abdominal segments; the right half is dorsal, the left ventral. (*2*) Leaflet of palmate tuft. (*3*) Leaflet of hair 1 of metathorax. (*4*) Leaflet of hair 1 of second abdominal segment. (*5*) The spiracular apparatus, dorsal view. (*6*) Sixth and seventh abdominal segments; right dorsal, left ventral. (*7*) Dorsal view of head. (*8*) Ventral view of head. (*9*) Tip of antenna. (*10*), (*11*), (*12*) Basal tubercles of pro-, meso-, and metathoracic pleural hairs. (*13*) Inner clypeal hair. (*14*) Anterior part of the frontoclypeus. (*15*) Tip of left maxillary palpus. (*16*) Lateral aspect of eighth, ninth, and tenth abdominal segments. (After Hurlbut.)

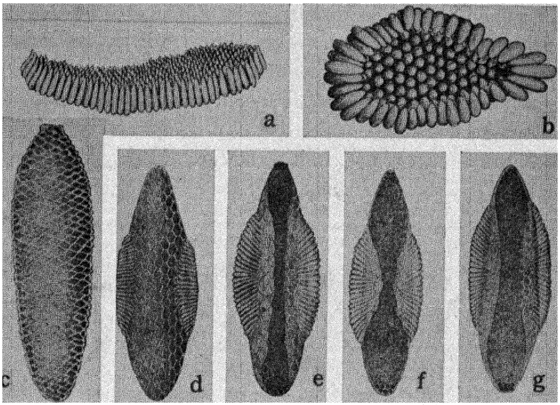

Fig. 111. Eggs of various species of mosquitoes. (*a*) Egg mass of *Culex pipiens.* (*b*) Egg mass of *Culiseta inornata.* (*c*) Egg of *Aedes aegypti.* (*d*) Egg of *Anopheles punctipennis,* dorsal view. (*e*) The same, ventral view. (*f*) Egg of *Anopheles quadrimaculatus,* dorsal view. (*g*) Egg of *Anopheles crucians.* (From Howard, Dyar, and Knab.)

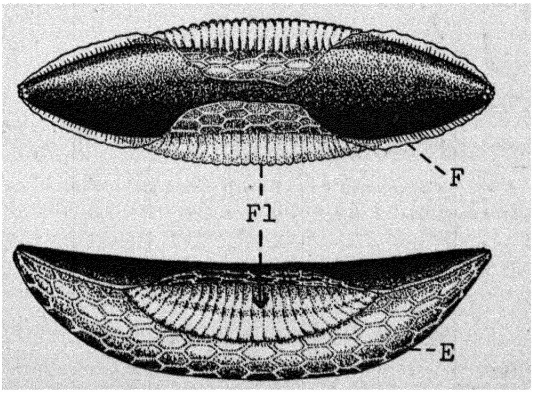

Fig. 112. Egg of *Anopheles walkeri.* E, chorion; F, frill; Fl, floats. (From Hurlbut.)

oval and may be laid singly (as in *Aedes*) or in masses (as in many *Culex* spp.). The eggs of anophelines are strikingly different from those of the culicines. The egg is generally boat-shaped, flattened, slightly convex or concave dorsally, and strongly convex ventrally (Fig. 112). The chorion is modified to form a frill, which partially or completely surrounds the upper portion.

In addition, a pair of characteristic floats or air sacs on each side enables the egg to float freely on the surface of the water (Fig. 112 Fl). The extent, arrangement of the floats, coloration, and certain other features have all been studied and have been found quite valuable in identifying species of *Anopheles,* especially of closely related forms or races as *A. maculipennis* of Europe. Causey, Deane, and Deane (1944) have studied the eggs of thirty Brazilian species of anophelines and have been able to identify species on egg characters.

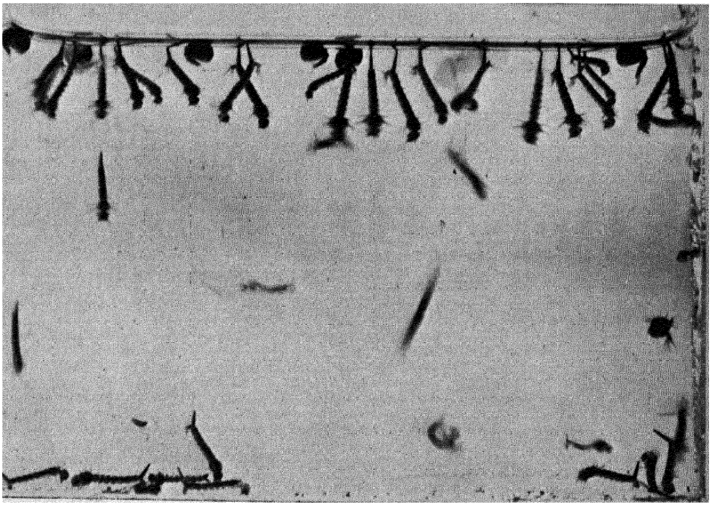

Fig. 113. Larvae of mosquitoes (*Aedes* spp.) resting and feeding at the surface of the water; note the long anal siphon or breathing tube; note the curled up pupae among them.

THE BIOLOGY OF MOSQUITOES

All mosquitoes undergo a complete metamorphosis, i.e., from the egg hatches a larva which feeds and grows; the larva, when mature, transforms into an active pupa (Fig. 113); from the pupa there later emerges the adult. The larval and pupal stages occur only in water (Fig. 113). The eggs of all known species are laid on water, near water, or in places where water is likely to be at some later date (as in many *Aedes* spp., *Psorophora* spp., and some others). All mosquito larvae molt four times, the last molt disclosing the pupa. In the study of the larva the fourth instar, which is the stage before the last molt, is called the mature larva, and it is this stage that is used almost exclusively for identification purposes. Studies on the earlier stages have been made, but not much success has resulted in identifying species except in certain small groups.

It is not our purpose here to give an extended account of mosquito bionomics. The literature in this field is so vast and has increased so enormously during the past few years that the reader must consult special papers dealing with groups or individual species. For our North American species consult King, Bradley, and McNeel (1942), Matheson (1944), or Carpenter, Middlekauff, and Chamberlain (1946). The following account is mainly concerned with those species known to be or suspected of being transmitters of important diseases.

CULICINE MOSQUITOES

The vast majority of our species belong in the tribes Culicini and Sabethini and are generally referred to as the culicine mosquitoes.

THE GENUS *CULEX:* Probably one of the most abundant, most widespread, and generally conceded most annoying mosquitoes is one that belongs to the genus *Culex,* the common house mosquito *Culex pipiens* Linn.[4] (Fig. 114). Not only is it annoying by its bites but it is the transmitter of several important diseases of man and other animals.

The house mosquito is widely distributed throughout the Holarctic region; in South America it is found south of the 39th parallel of latitude, in East Africa from Egypt south to the Cape and west to eastern Belgian Congo, in Madagascar, and probably in other regions. This species passes the winter as fertilized females, hibernating in various shelters such as attics, cellars, cowsheds, stables, and outbuildings of all kinds where protection, adequate moisture, and semidarkness are found. The males all die with the approach of winter. It is probable that, in the warmer portions of the range of this species, continuous breeding may occur, though at a much reduced rate as indicated by several recent workers. In the temperate regions hibernation is the general rule. Enormous numbers of females may pass the winter in very small shelters. I have estimated from careful counts of definite areas that over 100,000 hibernated in a small dark cellar not over four feet by six feet with a height of only

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[4] According to Marshall (1938) and other European workers this species rarely feeds on man but mainly on birds. They state that another species, so closely similar that it is difficult to recognize it, is the troublemaker. To this species has been assigned the name *Culex molestus* Förskal. This is the one that prefers mammalian blood but can reproduce generation after generation without blood ("autogeny"); *C. pipiens* requires blood for egg development and it prefers the blood of birds.

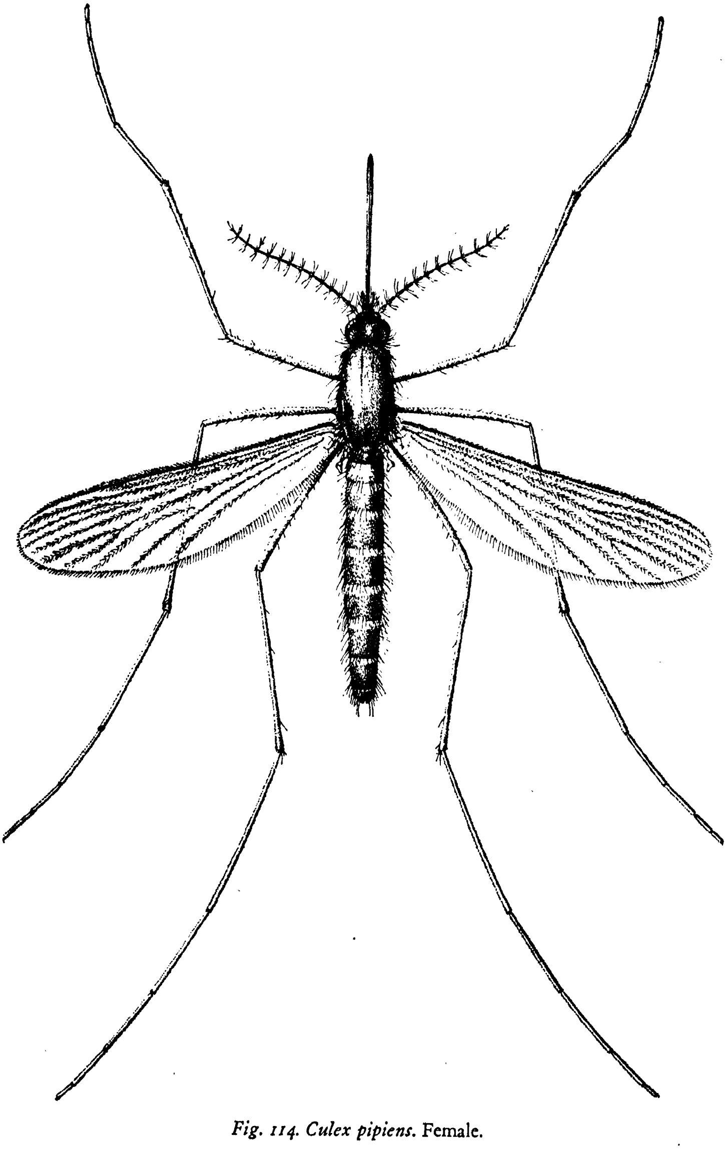

Fig. 114. Culex pipiens. Female.

seven feet. Scarcely a pin point could be found on which a mosquito did not cling to ceiling, walls, hanging ropes, and a pump, which occupied the center of the small room. During the cold weather the hibernating individuals show little activity though occasionally they may invade the warmer rooms in search of blood. With the approach of spring, activity is resumed and the females seek suitable places for oviposition. Depending on the locality, egg laying begins in May or June or possibly earlier. Each female deposits from 100 to

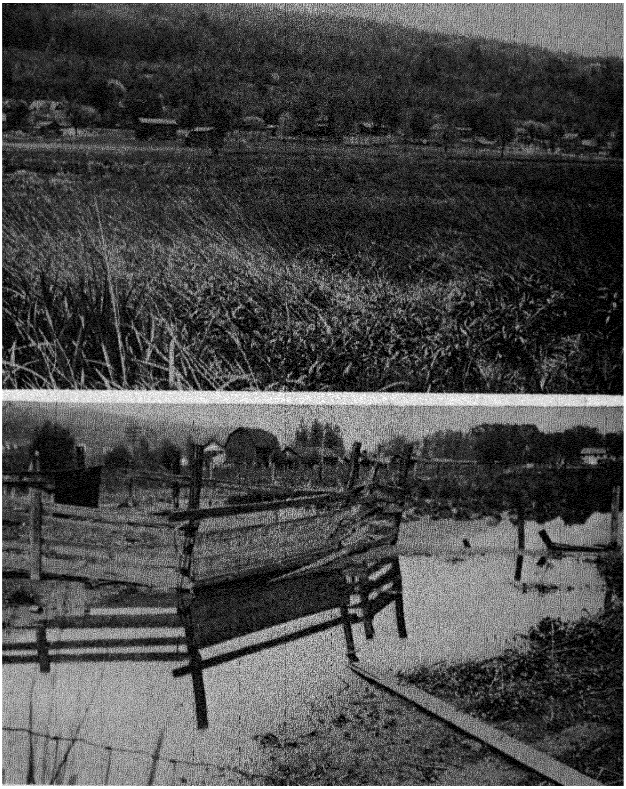

Fig. 115. Breeding places of mosquitoes. ***Upper:*** View across a marsh area with many pools and sluggish streams in which breed *Aedes vexans* and *Anopheles punctipennis*. ***Lower:*** A hog wallow where *Aedes vexans* and *Culex pipiens* breed in enormous numbers.

400 or more eggs in a boat-shaped mass (Fig. 111 *a*) on or close to the surface of standing water well protected from the winds. Each egg is cylindrical and tapers to the end away from the water. The favorite breeding grounds are rain-water barrels, cisterns, tanks, garden pools stocked with aquatic plants, slow-flowing polluted streams, flooded latrines, cesspools, polluted ponds (Fig. 115), catch basins, sagging gutters, and almost any water-filled container.

Depending on the temperature, the eggs hatch in from one to three days or occasionally longer. The young larva escapes from the lower end of the egg and swims actively about in the water. During warm weather the larval development is very rapid, the pupal stage being reached in seven to ten days. In cold weather, larval development may be greatly delayed. The larvae (Fig. 116) are very active, swimming with ease and rapidity by sudden jerks of the body. Being somewhat heavier than water, they rise to the surface by a rapid wriggling of the body from side to side, break through the surface film with their air tubes, and rest, the body sloping at an angle. During all this time, the mouth brushes are in motion, sweeping small particles into the alimentary canal along with a certain amount of water.

The pupal period is short, usually only two or three days. The pupa normally rests at the surface, the air tubes piercing the surface film. When disturbed, it swims rapidly downward by means of violent abdominal contractions. The tip of the abdomen is provided with two broad paddles, which greatly aid in pupal movement. Being lighter than water, the pupa, when quiet, rises to the surface again. As the time for the emergence of the adult approaches, the pupa, when disturbed, descends with difficulty and rises more rapidly. The time occupied in the transformation from pupa to adult is very short. The pupa will be seen to straighten out the abdomen and air appears between the pupal skin and the adult. The pupa now seems almost silvery white, and its specific gravity being greatly reduced, the whole cephalothorax and part of the abdomen touch the surface. The pupal skin now splits in the median line of the cephalothorax and the dorsum of the adult appears in the slit. By constant pressure the slit widens and two transverse slits appear on each side. Slowly the adult works its way out, using the pupal skin as a float and balancing itself with great care. In two or three minutes the insect, now swollen with engorged air, stands poised on its previous prison cell, and is soon ready for its initial flight. At first the adult is almost colorless, but in a few hours the permanent color pattern appears.

The entire life cycle from egg to adult occupies from 10 to 14 days. Generation after generation follows throughout the summer season and breeding only stops with the approach of cold weather. *Culex pipiens* may be found breeding

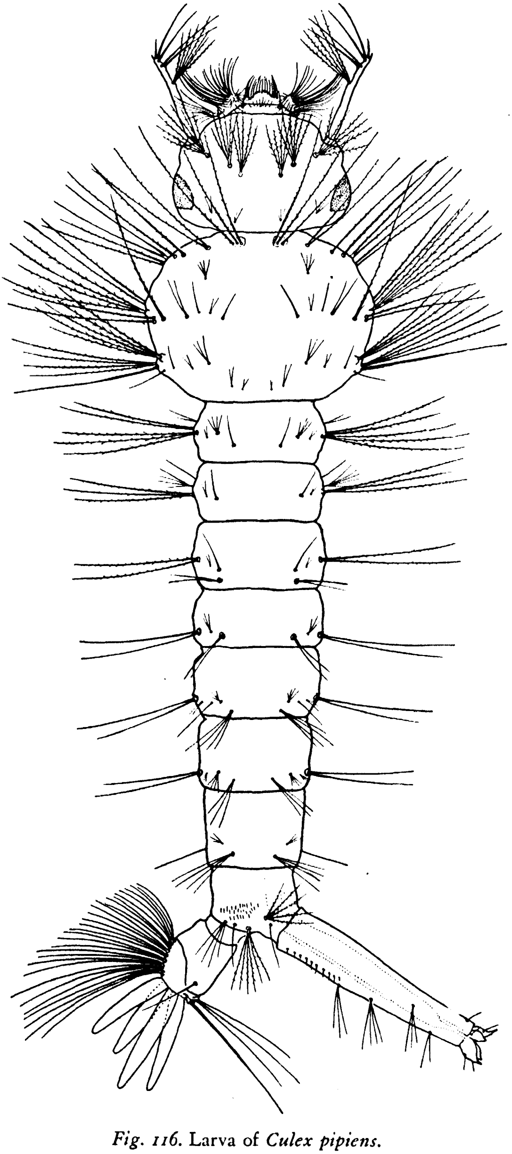

Fig. 116. Larva of *Culex pipiens.*

as late as November in the region of central New York. It is one of our domestic mosquitoes, that is, it breeds and lives in close proximity to human habitations.

In the tropical and subtropical regions of the world it is replaced by *Culex fatigans* Wied. (*quinquefasciatus* Say), a closely allied species. It is not always possible to separate these two species; reliance must be placed on a study of the male genitalia, and even this may not be satisfactory where the two species overlap. The larvae are practically identical. Both species breed in similar situations, invade houses, bite during the evening hours and at night. The tropical species is said to be intensely anthropophilic (NAVMED, 983. 1946) and has a recorded flight range of three to four miles.

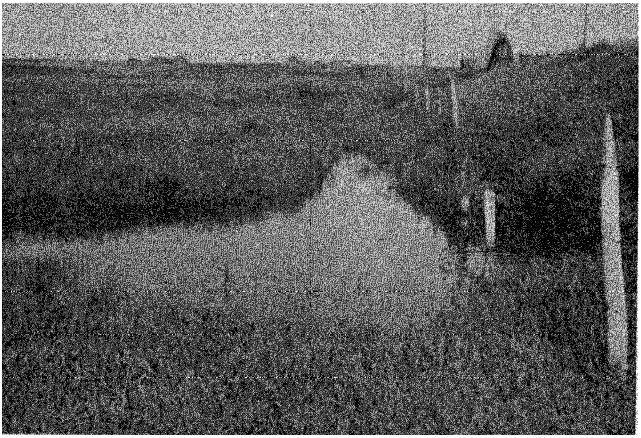

Fig. 117. A productive roadside pool in western Canada. In early spring *Aedes spencerii* is present, followed by *A. vexans* and *A. dorsalis;* later in August *A. spencerii, Culex tarsalis,* and *Culiseta inornata* are found. (After Rempel.)

Culex tarsalis Coquillett is easily recognized by the broad apical and basal white bands on the hind tarsi, the tibiae with apices and bases banded with white, and a broad whitish ring on the proboscis. In addition, the femora and tibiae have narrow longitudinal lines of white scales on outer and inner sides and a series of black V-shaped markings on the ventral surface of the abdomen. This is a very important species as it probably is the important vector of encephalitis of man and animals in North America. It has a wide distribution throughout the western United States and western Canada, especially in the plains. Freeborn (1926) reports it as the most widespread mosquito in California; Rees (1943) regards it as a major pest in Utah because of its abundance and wide distribution; Rempel reports it very abundant some years in Saskatchewan; Cox (1944) states it is widespread and abundant in Texas. Its general distribution is southern British Columbia eastward through the Canadian prairie provinces to Michigan, south through the central, southern, and western states and Mexico. The adults are fierce biters and readily enter houses, normally attacking at dusk and after dark. The common breeding places are in fresh or foul ground pools (Fig. 117), roadside ditches, irrigation water, rain barrels, and similar situations.

The genus *Culex* includes a large number of species placed in several subgenera. Many of the species are vectors of filariasis (see p. 562), some of Japanese B encephalitis as *Culex pipiens pallens* and *C. tritaeniorhynchus* (natural infection), others of St. Louis encephalitis, western and probably eastern encephalomyelitis of horses, and encephalitis of man. However, most of the species of *Culex* occur in the tropical and subtropical regions, and the relation of these species to their hosts, in most cases, is not known. Edwards (1932) listed 317 species, and since then over 100 new species have been described, but comparatively little is known of their biology.

THE GENUS *AEDES:* This genus contains a large number of species. In 1932 Edwards listed some 410 species, and since then over 100 new species have been recognized. The species are frequently abundant, and the adults may occur in vast numbers, especially in the Arctic regions, the subtropical regions, and the north temperate zone. They are distributed from the polar regions to the tropics and to high elevations in mountainous areas. Certain species as *A. sollicitans* and *A. taeniorhynchus* (breeding in tidal areas along seacoasts); *A. stimulans, A. excrucians, A. punctor, A. communis,* and others (in north temperate wooded areas); *A. vexans, A. sticticus,* and *A. lateralis* (some of our flood-water species); *A. spencerii, A. dorsalis, A. campestris* (on the open plains); *A. nearcticus* and *A. nigripes* (in the Arctic regions); and *A. ventrovittis* and others (in high mountainous regions) often render life almost unendurable at certain seasons of the year. Not only do *Aedes* species act as pests, but a goodly number serve as efficient vectors of diseases of man and animals (see Table 8).

It is not easy to briefly summarize the biology of the numerous species included in this genus. Edwards (1932) has given a general summary based on the various subgenera that he recognizes. In brief we may say the eggs are spindle-shaped or elliptical, thick-shelled, resistant to drying to a marked degree, and laid singly not on or in water but in places where water will be either by rains, melting snows, tidal areas, or flood waters, in tree holes, bamboo stumps, etc. As the eggs are very resistant they may lie dormant for several years (as for example A. *vexans* and *A. sticticus*). The larvae occur in various types of breeding places, and such places can be largely indicated by knowing

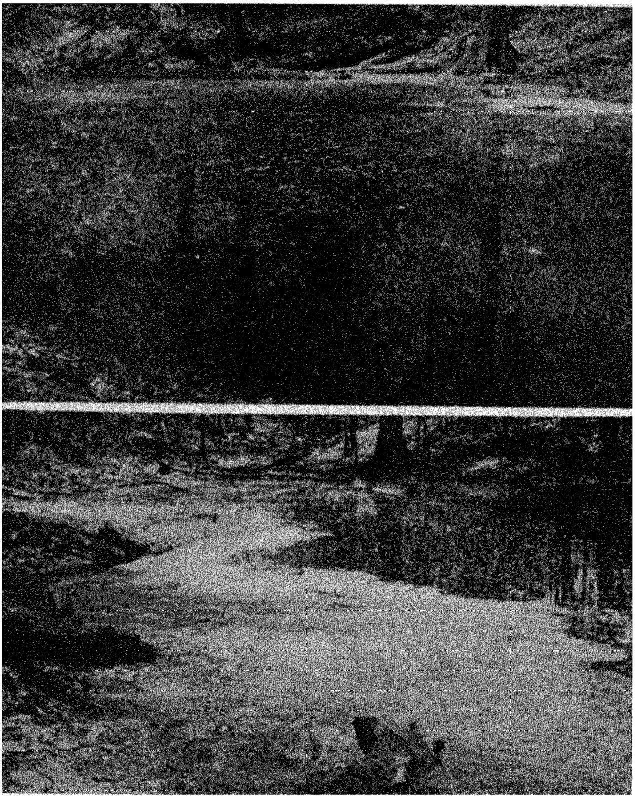

Fig. 118. Upper: A deep woodland pool in which *Aedes stimulans, A. fitchii,* and *A. excrucians* breed in immense numbers. *Lower:* A shallow woodland pool where *Aedes stimulans, A. fitchii, A. excrucians, A. intrudens, A. trichurus,* and *A. canadensis* breed.

the subgenus to which the species belongs. Most of the larvae are bottom feeders though a few are predaceous (species of the subgenus *Mucidus*).

The species of the subgenus *Ochlerotatus* are world-wide in distribution, and they breed in temporary ground pools formed by rains, melting snows, flood waters, and tidal marshes; a few in tree holes. Examples: *A.* (*O.*) *taeniorhynchus* and others in tidal marshes in the Americas; *A.* (*O.*) *vigilax,* coastal areas of Australia and nearby islands; *A.* (*O.*) *mariae* in sea-water pools along the Mediterranean coasts; *A.* (*O.*) *stimulans, A.* (*O.*) *fitchii, A.* (*O.*) *communis, A.* (*O.*) *trichurus,* and others in snow-water pools in northern North America (Fig. 118). In the subgenus *Finlaya* practically all the species breed in tree holes (Fig. 119), bamboo stems, leaf bases of various plants, potholes in stream beds, coconut husks, banana stumps, pitcher plants, and a few species from grassy pools. Examples: *A.* (*F.*) *triseriatus, A.* (*F.*) *alleni,* and *A.* (*F.*) *varipalpus* in North America, and many species in practically all parts of the world. The subgenus *Stegomyia* is practically confined to the tropical and subtropical regions of Africa, the Oriental region, and the Australasian region, though certain species, as *Aedes* (*S.*) *aegypti,* have been carried by commerce to nearly all parts of the world where they can find satisfactory breeding grounds. This subgenus was rather extensively studied in the western and southwestern Pacific regions during the recent war. Many new species have been described and old species broken down into a number of distinct species. Edwards (1932) lists 41 species from the world, and some 20 new species have since been described. This is an important group of mosquitoes. The principal breeding places are tree holes, leaf bases, coconut shells, artificial containers (as in *A. aegypti*), and similar situations. The adults of most species are day fliers. Though the subgenus *Aedimorphus* has over 50 species, only one is of

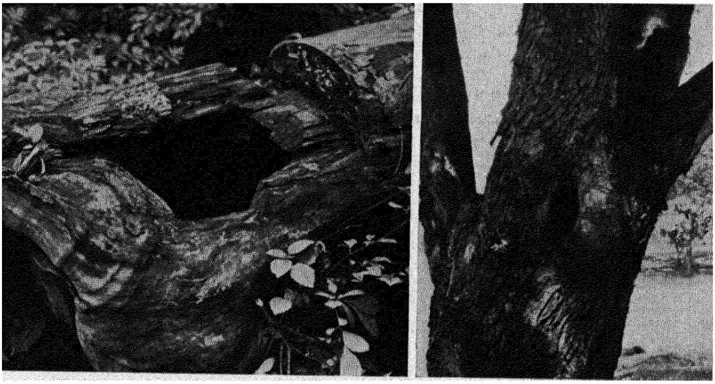

Fig. 119. Left: A sycamore log which was cut for the honey; now filled with water. In this tree hole breed *Anopheles barberi, Aedes triseriatus, Culex apicalis,* and *C. restuans. Right:* A tree hole in which *Aedes triseriatus* breed. (Both at Ithaca, New York.)

major importance. *A.* (*A.*) *vexans* is world-wide in distribution and a pest wherever it occurs in abundance. Most of the species breed in temporary ground pools or flood waters. The subgenus *Aedes* occurs primarily in the Oriental and Australasian regions. Only one species, *A.* (*A.*) *cinereus* occurs in Europe and America. It breeds in early spring pools. The other subgenera consist of few species and very little is known about them.

Aedes (*Stegomyia*) *aegypti* Linn. (*Stegomyia fasciata, Aedes argenteus, Aedes calopus,* etc.): The yellow-fever mosquito (Fig. 120) is probably the most domesticated of any species; it is found only about human habitations and primarily lives in our houses. It has a wide distribution in the tropical and subtropical regions. It is found in most countries lying between latitudes 45° North and 40° South, and its presence in temperate regions beyond these limits is of a temporary nature. According to Howard, Dyar, and Knab (1912), "Its permanent distribution is determined by the minimum temperatures and its temporary distribution by the maximum temperatures of any given region wherever it is sufficiently populated." Carter (1931) agrees with this view. The minimum temperatures are those that kill the hibernating eggs or prevent their development, and the maximum temperatures are those that permit the larvae to develop and the adults to flourish. Carter does not give these ranges of temperatures, though it is generally stated that in those areas where the nights are cool (68°F. and below), as in California, the mosquito does not occur even if in the daytime the temperatures are sufficiently high to be subtropical. Hindle gives the permanent distribution as confined between the two isothermal lines of 20° C. (68° F.).

The species can be recognized easily by the characteristic curving white lines on the thorax and the white banding of the tarsi. Though it has generally been considered an American species that has spread by way of commerce to all parts of the tropics, many workers now concede that it was originally an Ethiopian species brought to the Americas by the early navigators. The place of origin is of significance with regard to the origin and spread of yellow fever.

LIFE HISTORY: The eggs (Fig. 111 *c*) are laid singly on the water, just at the edge of the water, or on the sides of the container above the surface of the water. As the eggs can withstand drying for a long time, at least over five months, the filling of the receptacles by rain or otherwise assures the young larvae an adequate water supply for their short larval life. The eggs hatch in two days or less, if the temperatures are high, but hatching may be prolonged when the weather is cool, as during the winter months. The larval life is comparatively short, occupying six to ten days, or it may be greatly prolonged by

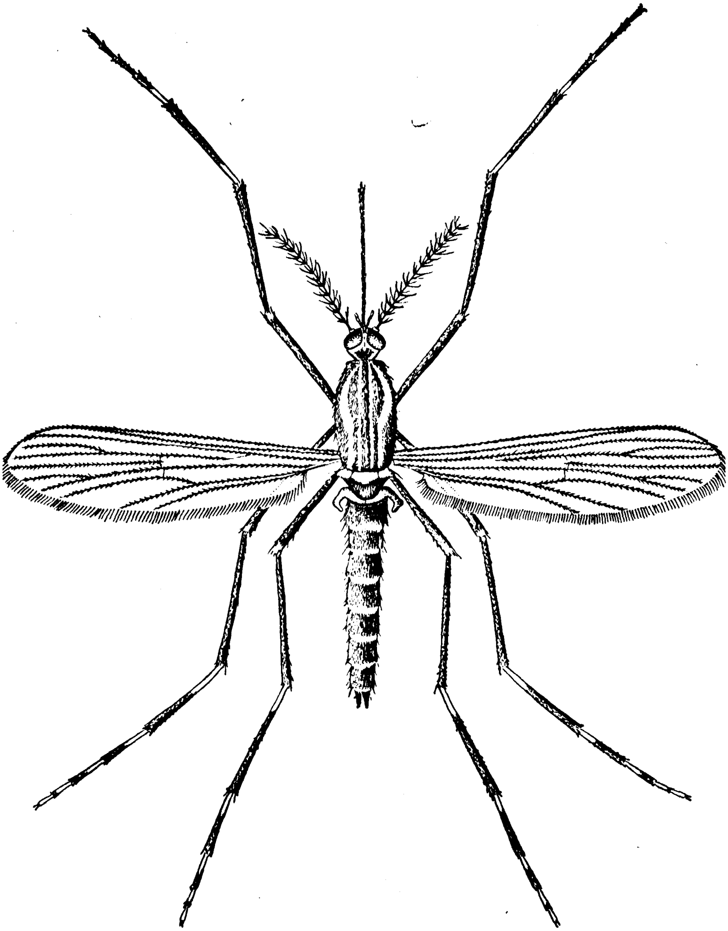

Fig. 120. The yellow-fever mosquito, *Aedes aegypti.*

cool weather. The mature larva (Fig. 121) is robust, rather stout, with a comparatively short, somewhat pointed siphon. The siphon bears a pair of small hair tufts just beyond the pecten. The scales (8 to 12) of the comb are rather distinctive—sole-shaped with a long, curving apical spine and several subapical spines (Fig. 121 2). The larvae are very responsive to disturbances of any kind, darting to the bottom of the water at the slightest disturbance or from a passing shadow. On account of this habit their presence is often diffi-

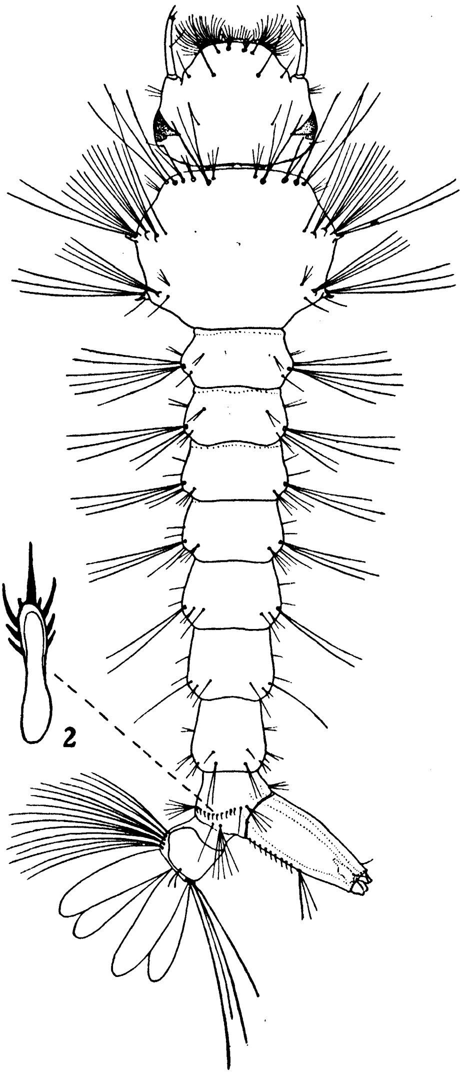

Fig. 121. Larva of the yellow-fever mosquito, *Aedes aegypti.* (2) One of the teeth from the comb, greatly enlarged.

cult to detect unless the inspector can take time to observe them as they quietly return to the surface or unless he empties out the container. Even then they may be missed as the larvae press themselves close to the bottom and are not easily dislodged. This burrowing habit frequently enables them to breed continuously in containers of drinking water which are frequently emptied and refilled, since many of them escape being poured out.

The pupal period is very short, not over two days under normal conditions. The entire life cycle may be passed in ten days, though ordinarily the time required varies from eleven days to three weeks. Within its permanent range it breeds throughout the year; generation succeeds generation with great rapidity when water, the necessary warmth, and a blood supply are available. During the colder months of the year the reproductive rate is slowed down or the eggs may remain dormant for a considerable period; the dry season may be passed in the egg stage.

The adults, on emerging, mate within a few hours or a few days. Mating takes place while in flight. The female must now secure a blood meal in order that her eggs may develop. If blood cannot be obtained the eggs remain undeveloped even though she feeds on honey, nectar, etc., and continues to live for a long time. The obtaining of a blood meal initiates ovarian development, and a steady source of blood enables the females to produce the maximum number of eggs. Each female is capable of laying from 50 to as many as 150 eggs during her lifetime. The females actively seek blood. They are primarily diurnal in their feeding habits and bite in bright sunlight. The times of greatest activity are the morning and evening hours, though I have had them feed on me consistently after dark in a lighted office where we were breeding them in quantity. The song of the yellow-fever mosquito is very feeble and it prefers to attack under cover, as about the ankles, under coat sleeves, at the back of the neck, and in similar places.

The adults can remain alive for long periods, at least nearly four months or even more, when properly fed and kept under conditions ensuring moisture and warmth. The length of the adult life is of great importance in relation to the spread of yellow fever. In the open the adult life is probably not so prolonged as four months, but on this point we have no very exact data. The range of flight is another important problem. It has generally been held that they do not fly over 100 yards from their breeding. Dunn (1927) records this species as breeding in water containers 500 yards from any habitation; this would indicate a flight range of at least that distance. Shannon and Davis (1930), in a series of well-planned experiments, obtained a flight range of 300 to 350 meters (13 mosquitoes captured); 950–1000 meters (7 mosquitoes taken); a full 1000 meters (1 mosquito obtained). In these experiments some 32,000 adults were employed and less than 0.4 per cent were recovered.

BREEDING PLACES: The primary breeding place is in water held in artificial containers in and around human habitations. These mosquitoes never breed in swamps, pools, or temporary puddles, even though these are located near houses. The more common types of water containers are rain-water barrels, wells, cisterns, tanks, sagging roof gutters, water-closet tanks, tin cans, vases with flowers, urns in cemeteries (Fig. 122), etc., in fact, in any type of artificial container capable of holding water; they also breed in tree holes (probably their original breeding ground), holes in stumps, water held by bromeliads, in the still-folded leaves of banana plants, and in similar situations. Dunn (1927) found them breeding in such numbers in tree holes (and some of the tree holes were at least 300 yards from houses) that he considered this type of breeding ground of importance in control work. He also found that the eggs could remain viable in tree holes throughout the entire dry season in West Africa. He discovered them breeding in the water pockets at the bottom of crab holes about lagoons. It is said that the females prefer clean water for oviposition purposes, but the larvae have been found in nearly all types of polluted water. It would seem that water containing leaves is very attractive (Dunn). Though this species breeds almost exclusively in fresh water, it will occasionally breed in brackish water. Garnham *et al.* (1946) report finding it commonly throughout the forests in parts of Kenya breeding in rock holes along river beds in dry weather and in holes in recently felled trees. They further state that it is not common about human habitations in this region.

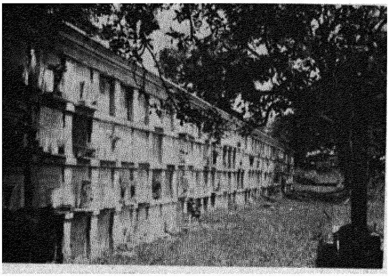

Fig. 122. View of a burial ground in the southern United States. In each niche are one or two flower vases, and *Aedes aegypti* breeds in them whenever water is present.

Aedes (*Stegomyia*) *albopictus* (Skuse) is an important species widely distributed in India west to the Caspian Sea, east throughout Burma, Indo-China, and the East Indies to New Guinea, and north through China to Manchuria; it also occurs in Japan, the Philippines, the Marianas, Hawaii, Madagascar, and Mauritius. Like *A.* (*S.*) *aegypti* it is being rapidly distributed by commerce. It can usually be recognized by the narrow median silvery-white stripe extending nearly the whole length of the mesonotum, the white flat scales on the lobes of the scutellum, the broad white rings on all segments of the hind tarsi, and the white scales on the pleura of the thorax arranged in patches rather than in lines (Fig. 123). This species is largely dominant in its range and it can usually be recognized from the *scutellaris* group by the white scales in patches instead of in broad lines on the pleura of the thorax.[5] *A. albopictus* is largely found about human habitations; it occurs up to 6000 feet in India and is reported breeding extensively in wooded areas in the lower mountain ranges of Hawaii. The adults are strongly anthropophilic and are persistent in their attacks. Though they usually bite outdoors during the twilight hours or in shady places during the day, yet the females readily enter buildings for a blood meal. This species breeds primarily in bamboo and tree stumps, tree holes, leaf axils, and coconut shells, and rarely in rock pools or artificial containers. The breeding grounds are usually about human dwellings. Throughout its range it is an effective vector of dengue and it has been shown to be experimentally a vector of yellow fever.

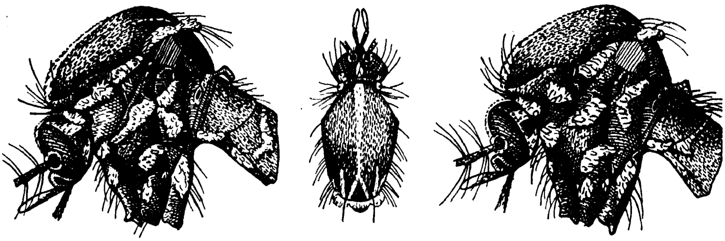

Fig. 123. Left and center: Lateral and Dorsal views of the thorax of *Aedes* (*Stegomyia*) *scutellaris. Right:* Lateral view of *Aedes* (*S.*) *albopictus.*

Aedes (*Stegomyia*) *scutellaris* (Walker) [*A.* (*S.*) *hebrideus* Edw. is the same species] occurs in New Guinea, New Hebrides and probably on many other Pacific islands. Its breeding grounds are quite similar to those of *albopictus* though it also uses any available artificial containers. The adults are vicious biters and seem to prefer human blood. It is considered to be a vector of dengue (Daggy, 1944) and it is reported to be naturally infected with *Wuchereria bancrofti.*

Aedes (*Stegomyia*) *simpsoni* Theobald is an important semidomestic mosquito. It breeds in tree holes, bamboo and leaf axils in banana plantations, and similar situations. In northern Nigeria it was found to pass the dry season as eggs in its breeding places. In Uganda this mosquito is very common and yellow-fever virus was isolated from wild-caught specimens in 1941 (Smithburn and Haddow, 1946); it is known to be an important vector. This mosquito has a wide distribution in Africa from Gambia on the west to Abyssinia and south to the Transvaal wherever breeding conditions are favorable. According to Haddow (1945), the female is almost exclusively diurnal in its biting habits.

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[5] Unfortunately there are a number of species, usually not very abundant, similarly marked. These can only be identified by an examination of the male genitalia.

Aedes (*Stegomyia*) *africanus* Theobald is another species widely distributed in Africa and has recently been incriminated as a probable vector in maintaining yellow-fever virus among the native monkeys and possibly other animals. Smithburn and Haddow (1946) have shown this species to be the dominant arboreal form in Bwamba, Uganda, and it lives and feeds in the tree canopy. It attacks throughout the day, though the biting peak is during the early evening hours.

Aedes sollicitans Walker is our famous salt-marsh or "New Jersey" mosquito. It breeds in the great salt marshes from Maine to Florida and west to Texas along the Gulf shore, in the Antilles, Cuba, and Jamaica. The eggs are deposited in the moist marshes and they hatch when their breeding grounds are flooded by high tides or rains. Under favorable conditions the life cycle from egg to adult is only about ten days. Where conditions are favorable, breeding is continuous throughout the year; in the North the winter is passed in the egg stage. The females are vicious biters and frequently render life almost unendurable along the coastal areas. It also migrates considerable distances; at least 40-mile migrations are on record. Along the west coast from San Francisco south this species is replaced by *Aedes squamiger,* another troublesome salt-marsh breeder. In the interior *Aedes dorsalis* breeds in the saline, brackish, or alkaline pools found in the great plains. It also occurs in fresh water. It is one of the dominant species of the western plains of Canada and the United States. It has a wide distribution in North America, Europe, Asia, China, and is reported from North Africa. *Aedes taeniorhynchus* Wied. is another salt-marsh-breeding mosquito with an extensive range. It is reported as breeding along the coastal areas of North and South America, on the east reaching Connecticut and on the west Santa Barbara, California. It often occurs in enormous swarms, particularly in the southern portion of its range.

In our northern woodlands we have a number of species that breed in vast numbers in spring pools formed by melting snows and spring rains. These species hibernate in the egg stage, and there is usually only one brood a year; the adults appear in early spring and live during the greater part of the summer. The females are vicious biters, largely confining their attacks to those who invade their habitats, the woodlands. Here belong *Aedes stimulans* Walker, *A. excrucians* Walker, *A. punctor* Kirby, *A. communis* de Geer, *A. fitchii* F. and Y., and others. *Aedes vexans* Meig. is one of the most widespread and annoying species of the genus. Next to *Culex pipiens, C. fatigans,* and *Aedes aegypti,* it is the most widely distributed mosquito species. It occurs practically throughout the Palearctic, Nearctic, and Oriental regions. It breeds primarily in fresh-water marshes, swamps, flooded river bottoms, meadow pools, etc., and often occurs in immense swarms after spring or early summer freshets. It is capable of rather extended migrations and may become a pest of the first importance. Normally it does not frequently invade houses though it may do so. It readily attacks man and other animals. There may be several broods a season, each following the flooding of their breeding grounds. (For further information on the species of this genus, consult the various references at the end of this chapter.)

THE GENUS *ERETMAPODITES:* This genus deserves mention since Bauer (1928) demonstrated that *E. chrysogaster* Graham could act as a vector of yellow fever. It contains 18 species and 6 subspecies and all are restricted to Africa south of the Sahara Desert. One species occurs also in Madagascar. The larvae, as far as known, are predaceous and are found in leaf axils, fallen leaves, leafy pools, and snail shells in densely wooded or heavy vegetation areas and on banana plantations. The adults are active biters during the day in areas where larvae breed. Haddow (1946) states that they do not bite in the night or during twilight. As Africa is a reservoir of yellow fever, the importance of these mosquitoes in maintaining this reservoir among animals may be of more importance than is now known. Haddow (1946) reports the isolation of a virus closely related to Rift Valley fever from a mixed group of these species collected in an uninhabited rain forest.

THE GENUS *HAEMAGOGUS: Haemagogus* is close allied to *Aedes* though the species show many affinities to the sabethines. There are no very good characters to distinguish the genus, but their day-flying habits (normally at high elevations) and their bright metallic blue and green coloration will aid in recognizing them. The species occur from Mexico to Argentina and are restricted to the New World. The species are very difficult to identify and as yet we have no thorough study of the genus as a whole. However, Kumm *et al.* (1946) have presented a detailed study of the species they found in Colombia. As far as known the species breed in tree holes, coconut shells, rock holes, bamboo joints, artificial containers, or similar situations, and the adults are normally active during the middle of the day and usually at relatively high elevations in the tropical forests.

Haemogogus spegazzinii falco Kumm *et al.* is the most widely distributed species in Colombia, is regarded as an important vector of jungle yellow fever, has been found repeatedly naturally infected, and occurs abundantly in the jungle-fever areas. Furthermore it is the only species recorded by Kumm *et al.* (1946) with a hairy larva in Colombia. They further consider all references to *H. capricornii*[6] Lutz in this area to refer to the above species. *H. janthinomys* Dyar is also a synonym. Bates (1944) in an intensive study of *H. capricornii* (? = *H. spegazzinii falco*) in eastern Colombia confirmed the previous observations of Bugher *et al.* (1944) that this species is most active at high elevations (upper tree canopy) during midday and that its ground activity is increased by the cutting down of trees, thus increasing the light intensity of ground levels. This may explain the prevalence of jungle yellow fever among woodcutters.

ANOPHELINE MOSQUITOES

Anopheline mosquitoes are placed in at least three genera—*Chagasia,* with three or possibly four species known only from South America and Panama; *Bironella,* with some six to eight species known only from New Guinea, the Solomons, and nearby islands; and *Anopheles,* which is world-wide in distribution with nearly 400 species and varieties. The genus *Anopheles* has been divided into numerous genera, at least 38, but these are now regarded as synonyms though some of them are employed to indicate subgenera (Edwards, 1932, recognizes only four subgenera).

Anophelines can be distinguished from the culicines in all stages of their development. The eggs (Figs. 111,112) in all species are deposited singly or in small groups on the surface of the water and possess, in practically all species, lateral floats or air cushions. The larva (Fig. 106) does not possess a respiratory siphon and, when feeding, rests at the surface of the water and parallel to it (Fig. 124). The pupae can be recognized by the lateral spines (Fig. 104) being located at the lateral apical angles of the abdomen and normally are peglike except the last pair. The adults, both males and females in practically all species, have long palpi, usually as long as the proboscis (Fig. 125); the wings are usually spotted (Fig. 126); the scutellum is smoothly arcuate behind with hairs evenly distributed, never distinctly trilobed with hairs and scales on the lobes except in the genus *Chagasia.* Furthermore the adults, when at rest, hold their bodies at a distinct angle, 30° to almost 90°, while the culicines hold their bodies nearly parallel to the substratum (Fig. 127).

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[6] As all *Haemagogus* species can only be determined by the male genitalia or in most cases by larvae, it is interesting to note that no males of this species have ever been taken in the wild. Males were obtained by rearing from eggs obtained from captured females.

The structure of the eggs of anophelines has already been described. However, attention should be called to the recent studies of anopheline eggs and their use in recognizing species. In the case of *Anopheles maculipennis* complex Bates (1940) recognizes five species and two varieties based largely on egg characters, though minute differences can be found in the adults, their activities (anthropophilic or zoophilic), their hibernation, their failure to make successful crosses in certain cases, and certain minute larval and male structures. Yet in this important malaria-transmitting complex the most reliable characters for separating the species or races appear to be in the eggs. Certain of these species are important transmitters of malaria (see pp. 306, 343). In *Anopheles walkeri* the development of two egg types is a remarkable phe-

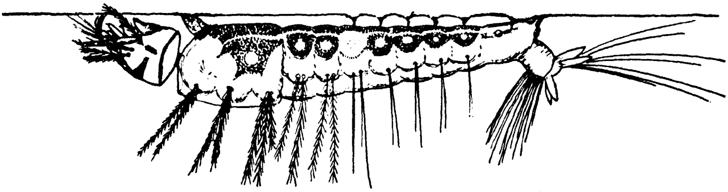

Fig. 124. Larva of *Anopheles* sp. resting and feeding at the surface of the water. Note the float hairs piercing the surface film and the thoracic lobe just behind the head attached to the surface film.

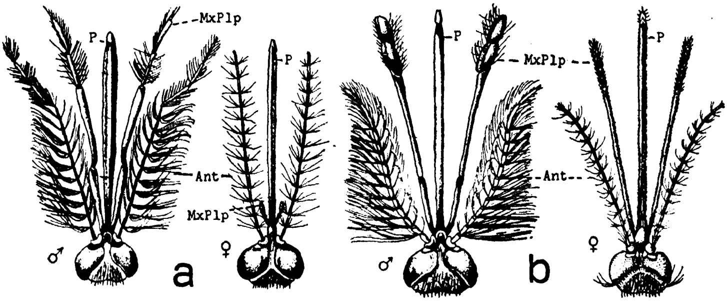

Fig. 125. The heads of mosquitoes. (*a*) Male and female heads of a culicine mosquito. (*b*) Male and female heads of an anopheline mosquito. Ant, antennae; MxPlp, maxillary palpi; P, proboscises.

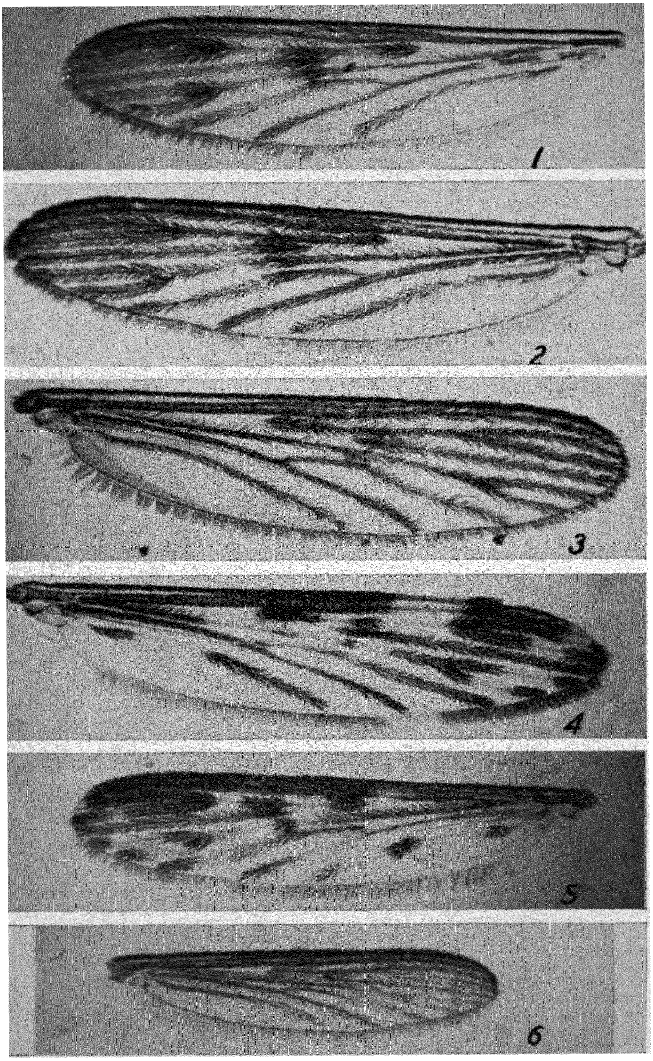

Fig. 126. Wings of American *Anopheles* spp. (*1*) *A. carlei.* (2) *A. quadrimaculatus.* (*3*) *A. walkeri.* (*4*) *A. punctipennis.* (*5*) *A. crucians.* (*6*) *A. barberi.*

nomenon—one type for summer breeding (Fig. 128) and a much larger, frost-resisting type (Fig. 128) for hibernation in the northern portion of its range. It is probable that some tropical species produce eggs that resist desiccation during the dry seasons (estivation) while the normal type is produced in the wet season. This seems to be indicated by the different illustrations of eggs of the same species by various authors. Unfortunately very little work has been done on this phase of mosquito biology. The eggs of most anophelines studied are not capable of withstanding much desiccation, a record of about 15 days being the maximum. However, the study of the eggs for identification purposes has shown interesting results. The work of Causey, Deane, and Deane (1944) on the eggs of 30 South American species shows their wide variety and the variations within a single species.

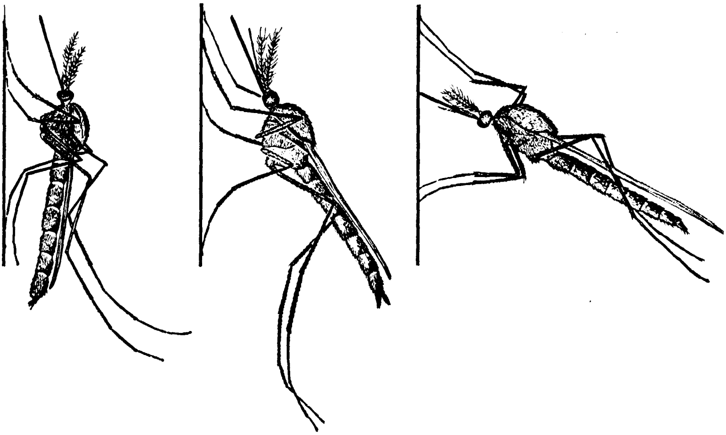

Fig. 127. The resting position of our common mosquitoes. *Left: Culex pipiens.* (All our common species except anophelines normally rest in this position.) *Center: Anopheles quadrimaculatus. Right: A. crucians.*

LARVAL HABITATS: It is not possible to generalize on larval habitats since many species would seem to have certain preferred breeding places though others readily accept any available aquatic situation suitable for larval development. In general, it may be said that anophelines rarely breed in open, wind-swept bodies of fresh water that are free of vegetation, along shore lines that are free of vegetation or debris, or in swift-running streams with clear margins, and not commonly in forest pools; a few species select saline pools or marginal areas along the seashore, and some species select tree holes or water in epiphytic plants, as bromeliads. Anophelines occur in nearly all parts of the world except in the Arctic regions and at high mountain levels. In general it may be said that breeding occurs between the summer isotherm of 60° North and between 60° and 70° of the southern summer isotherm. The *A. maculipennis* complex of the Old World has probably the most extensive distribution of any anopheline species. It occurs from Great Britain east through central Siberia to the maritime provinces and from Sweden and northern Russia south to North Africa and east along the northern portion of the Mediterranean through an extensive area of southern Russia to Mongolia, Manchuria, and Japan. If the North American varieties (?) are included, it has a still wider distribution. This species also occurs at considerable elevations. Its breeding grounds include fresh or brackish marshes, swamps, lagoons, rice fields, upland streams, cool fresh-water pools, ponds, and similar situations. The more common breeding places and distribution of the anopheline species which are known to be vectors of malaria are indicated in Table 7.

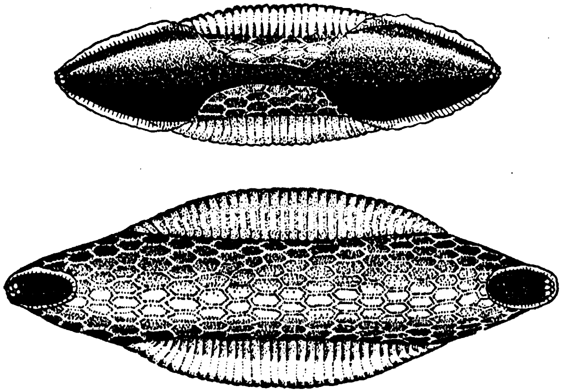

Fig. 128. Upper: The summer egg of *Anopheles walkeri. Lower:* Winter egg of the same species.

Most anophelines occur in the lowlands. However, many species occur up to median elevations (1000 to 2000 feet) and some at considerable heights. In North America *A. quadrimaculatus* occurs commonly near Ithaca at over 1200 feet; *A. earlei* has been taken at over 2000 feet; *A. freeborni* has been taken breeding at 7000 feet in Utah (Rees, 1943); 6000 feet in southern Idaho (Gjullin). In Mexico *A. parapunctipennis* and *A. pseudopunctipennis* occur commonly from 3000 to 6500 feet. In the Andean region Hackett (1945) reports *A. pseudopunctipennis* breeding at elevations of 2773 meters (about 8550 feet); it is the primary vector of malaria throughout the mountain region at elevations of from 250 to 2500 meters. *A. eiseni* has been taken up to 5000 feet. *A. argyritarsis* occurs from the lowlands to at least 5000 feet, and in Guatemala it abounds at 2000 feet. In Mexico *A. albimanus* occurs in the rainy season from the lowlands to over 3000 feet. In Venezuela Anduze (1943) reports *A. strodei* and *A. oswaldoi* as breeding up to 1600 feet, and *A. argyritarsis, A. eiseni, A. neomaculipalpus,* and *A. pseudopunctipennis* were taken up to 3300 feet. Between 3300 and 8200 feet *A. argyritarsis, A. pseudopunctipennis,* and *A. boliviensis* were found breeding. In Mexico *A. pseudopunctipennis* occurs from sea level to 7200 feet or more, while Shannon reports it in the Andes at 7800 feet.

In Africa *A. garnhami* occurs in the Kenya mountains to as high as 11,000 feet; *A. implexus* occurs from 3000 to 5000 feet, breeding in deep forest shade in swamps, springs, and seepages; *A. kingi* is reported breeding at 7000 feet; *A. gambiae* breeds from sea level to 7000 feet in Abyssinia, at 5100 feet in Arabia, and at 4000 feet in Uganda.

In India a long series of anophelines are reported breeding from 2000 to 11,000 feet. Christophers (1933) records the following species: *A. aitkeni, A. moghulensis,* and *A. jeyporiensis* are found from the plains to at least 6000 feet; *A. hyrcanus nigerrimus, A. turkhudi, A. annularis,* and *A. annandalei* go as high as 7000 feet; *A. maculatus willmori* occurs in the foothills of the Himalayas from 2000 to 8000 feet; *A. culicifacies* is reported even as high as 7500 feet; *A gigas gigas* usually occurs from 5000 to 6000 feet in southern India, while *A. gigas baileyi* has been taken at 11,000 feet in Tibet; *A. barianensis,* a tree-hole breeder, occurs from 5000 to 8000 feet in the northwest Himalaya region; *A. minimus* breeds abundantly at 2000 feet and occurs to at least 5000 feet; *A. fluviatilis,* a stream breeding species, occurs at elevations between 1000 and 7500 feet. Other species might be added to this brief list.

In the Australasian region *A. minimus* occurs from sea level to 3000 feet; *A. farauti* has been reported to as high as 2000 feet; and *A. stigmaticus* occurs to elevations of as much as 6000 feet.

THE ADULTS: It is not possible to give a general summary of the biology of the adults. Instead a brief summary of the biology of a few of the more important vectors of malaria with a discussion of the adults must suffice.

Anopheles quadrimaculatus (Say) (Fig. 129) is the most important vector of malaria in North America. Its distribution extends from New Hampshire and Massachusetts west through central New York and southern Ontario to Minnesota and Iowa, south throughout the southern states, and west to central Texas, Oklahoma, and eastern Kansas. It also occurs in eastern Mexico south to Veracruz. The adults are active during the evening, night, and morning hours and readily enter houses or other buildings in search of blood. They readily feed on man and wild and domestic animals. Normally they do not feed during the daytime, though they will attack in houses and out of doors during dark and cloudy weather. During the day they may be found resting in dark corners in buildings, underneath all kinds of houses, in stables and hollow trees, under bridges and culverts, in outdoor privies (one of the most common places), and in any shelter that provides darkness and moisture. The males and females mate shortly after emergence either after or before a blood meal. Keener (1945) describes the mating in small rearing cages as taking place about 8 P.M. They mate in flight, then usually fall to the bottom of the cage and separate after about 10 to 15 seconds (stenogamous species). A single

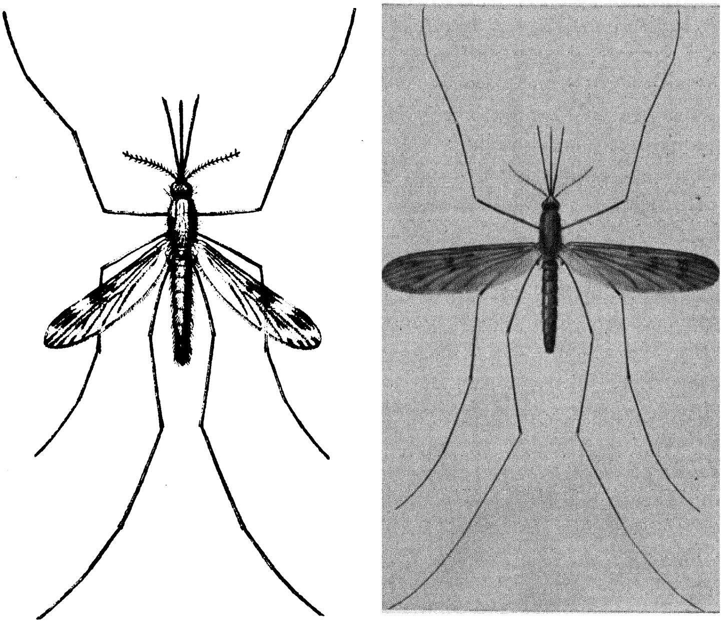

Fig. 129. Two of our common anophelines. *Left: Anopheles punctipennis. Right: A. quadrimaculatus.*

mating is sufficient to ensure fertile eggs during the life of the female. If blood meals are available oviposition takes place about three days after emergence. Keener records each female as laying 9 to 12 batches during its lifetime; each batch varied from 194 to 263 eggs. Three hundred females deposited 200,000 eggs during their life or an average of 660 eggs per female. Well-fed females apparently may lay from 2000 to 3000 eggs. Oviposition occurred during evening hours. The length of life of the female varied from 7 to 62 days, with a mean of 21 days; the males varied from a few days with a mean of 7 days. How long they may live in nature is not well known.

The breeding places are most commonly ponds, pools, grassy and weedy margins of lakes, swamps, and collections of water with floating debris or emergent or floating vegetation. It seems to prefer open, sunlit waters with debris or vegetation, though it breeds in water areas densely shaded by tall trees. During the summer season the larval period is comparatively short. The eggs hatch in from 2 to 3 days and the larvae complete their growth in from 12 to 19 days, depending on food supply and water temperature. The pupal period varies from 2 to 6 days. Hurlbut (1943) found the average period from egg to adult to vary from 18 to 23 days at an outdoor temperature of about 74° F. The number of generations per season varies according to the region studied. Boyd (1930) concluded there were seven to eight annual generations in North Carolina, and in southwestern Georgia eight to ten. Hurlbut (1943) records nine to ten generations in northern Alabama. Bradley and Fritz (1945) present an interesting account, based on extensive data, of the duration of the significant breeding season in each of the annual isothermal zones at 5° F. intervals (50° to 55°, 55° to 60°, 60° to 65°, 65° to 70°, and 70° to 75° F.) in the United States, and within each zone the average annual temperature varies only within 5° F. In the 70° to 75° isothermal zone breeding is continuous throughout the year, but in the 50° to 55° isothermal zone breeding occurs only from late May to the middle of October. In the northern portion of its range and at high elevations the females (the males die off) seek hibernating quarters in cool, dark places such as cellars, hollow trees, caves, and similar locations where there is a certain amount of moisture. In the warmer portions of its range true hibernation is regarded as doubtful since breeding may be continuous, and larvae have been taken in practically every month of the year. It is probable that in the cool season larvae succeed in withstanding considerable cold weather and that the larval development period is greatly lengthened, thus providing for rapid production at the beginning of warmer weather.

Anopheles freeborni Aitken (*A. maculipennis freeborni* Aitken) is widely distributed in North America west of the Rocky Mountains and extends from southern British Columbia south through western Montana, Utah, Colorado, and New Mexico to western Texas. Within this area its breeding grounds are restricted by more or less local conditions. In California it is widely distributed except along the north coast and is very abundant in the San Joaquin and Sacramento Valleys. In southern California it reaches the coast at San Luis Obispo. It is abundant in the Willamette Valley, Oregon, and Stage reports it breeding in abundance in irrigated hayfields in the arid section of eastern Oregon (Fig. 130). Rees (1943) indicates a wide distribution in Utah. He reports taking this species at an elevation of 7000 feet. According to Freeborn (1943), the breeding grounds are mainly small, insignificant fresh-water pools that are at least partially exposed to sunlight and where there is vegetative protection such as algae. Such places include hoofprints in seepage areas, small bays in streams, cutoff pools, roadside pools, and semipermanent pools in irrigation areas. It rarely breeds in foul water, artificial containers, or large bodies of water such as ponds or borrow pits or in swamps or wooded areas. Hardman (1947) has reared this species under artificial conditions and produced seven generations in seven months.

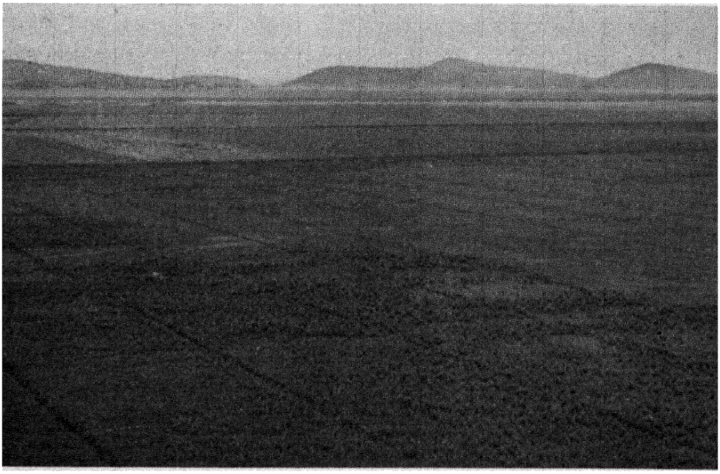

Fig. 130. Photograph of a 10,000-acre irrigated hayfield in eastern Oregon. Note the low section in the left-hand corner with weeds and water. Here breed *Anopheles freeborni, Aedes flavescens, A. dorsalis,* and *Culex tarsalis.* (Courtesy Mr. Stage, U.S. Bureau of Entomology and Plant Quarantine.)

He found maximum egg production in a wild-caught female to be 1527 whereas laboratory-reared females averaged 751.

The adults closely resemble *A. quadrimaculatus* but they can usually be separated by the markings of the mesonotum. In *freeborni* there is a rather distinct median, longitudinal, pruinose stripe, whereas in *quadrimaculatus* the mesonotum is uniformly dark without any indication of a median stripe. The larva of *freeborni* is practically identical with that of *punctipennis*. According to all recent workers, *freeborni* is the prime vector of malaria within its range. It is known to seek human blood, readily invades houses, and is a vicious indoor biter.

Anopheles occidentalis Dyar and Knab (*A. maculipennis occidentalis* and *A. maculipennis* of authors[7]) is apparently restricted to a coastal area stretching from Ventura Bay north to Washington and British Columbia. It has also been collected in Alaska and the Yukon, and Aitken reports it from Aklavik on the Mackenzie River at 69° North latitude. The eastern form listed under the above name is undoubtedly a distinct species and is described as *A. earlei* Vargas. Both species have the distinctive coppery or golden spot at the apex of the wing. Aitken (1945) does not give much information on the biology of this species, but apparently it is not abundant in its range and plays no part in the transmission of malaria. He does not report it as a house invader.

Anopheles earlei Vargas is a species based on the study of females from Wisconsin; the type male came from Cayuta Lake, New York. Here (elevation 1272 feet) it usually occurs in abundance, though its larval habitats have not been studied intensively. However, it can be separated in all stages from *A. occidentalis* as described by Aitken (1945). The females bite readily during the daytime but attack most vigorously during the twilight hours (till 9 P.M. at least). It readily invades houses and the females enter hibernation in situations similar to those of *A. quadrimaculatus*. Its distribution is not well known, though probably it is the species that extends from Maine south to New York and west along the United States and Canadian borders to the Rocky Mountains. It is definitely known from New York, Michigan, and Wisconsin. Preliminary experiments by Dr. Boyd indicate that this anopheline may be a vector of malaria.

Anopheles pseudopunctipennis Theobald is apparently a variable species

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[7] Aitken (1945) gives a detailed synonymic statement of this species, but his references to this species east of Wisconsin and Michigan and probably east of the Rocky Mountains do not refer to this species. See *A. earlei* Vargas below.

and may consist of several species or subspecies. The adults may be distinguished from closely related North American species by the whitish areas or spots (usually 2) on the costal margin of the wing, the fringe with pale spots at tips of veins, and terminal segment of the female palpus white. *A. franciscanus,* regarded by Aitken as a subspecies or variety, may be separated by the terminal segment of the female palpus not being entirely white but with an apical black ring. In the larval stage the presence of "tails" on the postspiracular plates of the respiratory apparatus is diagnostic throughout its range except in many parts of California where the "tails" are lacking. This anopheline (or its varieties) is probably the most widely distributed species in the Americas and occurs from about 42° North latitude in the western part of the United States through Mexico, Central America, Panama, Colombia, Venezuela, and south to northeastern Argentina (Cordoba, 31° South) and Chile (Pica, 20° 30′) following the foothills on both sides of the Andes. It also occurs in Trinidad and Grenada. According to Aitken (1945), this species prefers arid canyons and valleys where the larvae occur in the small, clear, slow-moving streams and side pools of receding rivers containing a rich growth of algae and exposed to the sun. Barber reports it breeding also in cool pools in the shade in New Mexico. In Mexico it commonly occurs in shaded pools with algae. Its preference seems to be in more or less exposed waters with abundance of algal growth. According to Rees (1943) the females hibernate, and he found them commonly in outbuildings and human dwellings in southern Utah. The relation of this variable species to malaria is discussed on pages 341–343.

Anopheles punctipennis (Say) (Fig. 129) is the most widespread anopheline in North America. It ranges from southern Canada south to the Gulf of Mexico and reaches the Mexican plateau (state of Hidalgo); west of the Rocky Mountains it ranges from British Columbia south through Washington and Oregon to southern California; it is rare or not found in most of the mountain states. In the east its breeding places are varied—rain-water barrels, roadside puddles, ruts in muddy roads, grassy bogs, swamps, hog wallows, spring pools, margins of streams, lakes, and open ponds. The writer has recently taken it in deep woodland pools (October, 1945). The adult females hibernate in cellars, houses, outbuildings, and similar situations. Frequently during the winter they will invade sleeping rooms and bite. The females usually attack during the twilight hours and when abundant readily enter houses and seek blood.

Anopheles crucians Wied., *A. bradleyi* King, and *A. georgianus* King constitute a complex that presents many difficulties. *A. crucians* occurs from

Massachusetts south through the eastern states to the Gulf of Mexico and west to western Texas and north to Illinois and Kentucky. It breeds almost exclusively in acid waters. *A. bradleyi* ranges along the Atlantic coast from New Jersey to Veracruz, Mexico. It normally breeds in saline pools. *A. georgianus* has been taken in Georgia, Alabama, and Louisiana and breeds in fresh water. Though these species, at least *crucians,* readily bite humans, they are not considered of any importance as vectors of malaria. Sabrosky *et al.* (1946) report 3.38 per cent infection in November with *Plasmodia* in South Carolina, and these species may play a more important role than is now recognized.

Anopheles walkeri Theobald is widely distributed in the eastern half of the United States west to Minnesota and western Louisiana. It is a fierce biter, attacking principally during twilight hours. If disturbed it will attack during the day. It is attracted to lights and is frequently taken in numbers at light traps. It is the only known anopheline that hibernates in the egg state in the northern part of its range.

Anopheles atropos Dyar and Knab is a salt-water breeder and occurs along the Atlantic coastal area from New Jersey to Texas and is reported from Cuba. *Anopheles barberi* Coquillett breeds in tree holes (Fig. 119) and is our only North American anopheline that hibernates as young larvae frozen in the water. It is a very small species. It is widely distributed in the eastern half of the United States north to Iowa and New York. It has been shown capable of infection with *Plasmodium vivax* and did transmit the infection from the sick to the well (Stratman, Thomas, and Baker, 1936).

The subgenus *Nyssorhynchus* is restricted to a region extending from Mexico, through Central America, to South America and most of the West Indies. Only a single species, *A.* (*N.*) *albimanus* Wied., occurs in the United States, and it is known only from a small area in southeastern Texas around Brownsville and in southern Florida. These are frequently called the "white-footed" anophelines because the last three segments of the hind tarsi are nearly all white. Lane (1939) lists 17 species in this subgenus from the neotropical region but today the total is probably greater. Causey, Deane, and Deane (1946) recognize 11 species composing the *tarsimaculatus* complex in northeast Brazil. This would give us over 25 recognized species. In this group the male genitalia is characteristic—only one basal spine on a tubercle on the sidepiece with two other spines inserted near the middle. The larvae do not seem to be characterized as a group or easily separated from the subgenus *Anopheles.* In this group are many important vectors of malaria. These include *A. albimanus, A. darlingi, A. albitarsus,* and *A. aquasalis.*

Anopheles (*Nyssorhynchus*) *albimanus* Wied. has a wide distribution in Mexico, Central America, Panama, the West Indies, Colombia, Ecuador, and Venezuela and also occurs in Texas and Florida. The adults are persistent invaders of dwellings and are avid feeders on man, though they attack horses and other animals. They are primarily nocturnal and definite flights are recorded in Panama. These flights occur in the early evening hours and usually last 30 to 45 minutes. During the night the mosquitoes remain in houses but leave in the early morning hours for other shelter (the writer has seen adults [7] taken in a native Mexican hut full of blood about 11 A.M.). Collection of this species while it is resting during the day in native huts is common in the state of Veracruz (Mexico). Extensive migration of this species has been recorded and flights of 12 miles or more have been noted in Panama. The principal requirements for breeding places are sun, vegetation, and little or no movement of water. It breeds extensively in clear pools, slow and stagnant streams, tracks in pastures, open ponds, swamps, seepage areas, potholes, ditches, road ruts, and lakes with surface vegetation; it also breeds in brackish pools open to sunlight. Normally this species is restricted to the lowlands throughout its range, though in the rainy reason it breeds abundantly at over 3000 feet in Veracruz. It is one of the important vectors of malaria.

Anopheles (*N.*) *darlingi* Root was described from the state of Rio de Janeiro in 1926 and is known as an excellent vector of malaria. Its distribution is from Argentina to Venezuela; it also occurs in British Honduras and Guatemala. Recently (1943) it has been found in the state of Chiapas, Mexico, and more recently (1946) in the state of Tabasco. It undoubtedly will spread along the coast line of the Gulf of Mexico and should easily gain access to the southern United States. Its favorite larval habitats are among mats of vegetation in shaded, clear, fresh water of lagoons, overflows, and floodwaters as in the Amazon Valley. According to Shannon (1933), this species is primarily a lowland breeder and is associated with floodwater conditions. The adults are consistent invaders of houses and prefer human blood. Bates (1947) and Sigioli (1947) report that this species breeds readily under artificial conditions.

Anopheles (*N.*) *aquasalis* was described by Curry (1923), who separated it from the so-called *tarsimaculatus* complex. It is a brackish water breeder and appears to be quite restricted to shaded or open brackish tidal swamps, especially along tidal river areas, on the Atlantic side of Panama, Nicaragua, Trinidad, the lesser Antilles, and as far south as Pernambuco and Algoas in Brazil. It is also recorded breeding inland (10 miles) in the rice fields of Trinidad. The adults feed freely on animals and man and readily enter houses. However they leave their feeding grounds before dawn and are rarely found in buildings during the day. Throughout its range it is an important vector of malaria.

Anopheles (*Kerteszia*) *bellator* Dyar and Knab is an interesting anopheline as its only known breeding places are the contained water in epiphytic bromeliads. It occurs in Trinidad and Venezuela. In Trinidad this mosquito breeds abundantly in the water collected in bromeliads on the immortelle (*Erythrina*), which is used as a shade in the cocoa plantations, and on other trees on the highlands. The adults are anthropophilic, attacking humans during the evening hours (5 to 8 P.M.); they seek human habitations but leave immediately after feeding; they also feed in the early morning hours. The observations of de Verteuil (1925–1937) that this anopheline, on epidemiological evidence, is an important vector of malaria in Trinidad have been abundantly confirmed by Rozeboom and Laird (1942) and Downs, Gillette, and Shannon (1943).

Anopheles gambiae Giles is probably one of the most effective transmitters of malaria in regions where it and malaria are present. It occurs over most of tropical and subtropical Africa where breeding conditions are favorable from the Sahara Desert south to Natal. On the eastern side of Africa it is abundant in Ethiopia and Eritrea and occurs north to Khartoum and southern Egypt. It occurs in Arabia and the islands of Mauritius, Reunion, and Madagascar. This anopheline is primarily a small pool breeder, frequenting such places as puddles, shallow ponds, animal footprints, roadside ditches, irrigation furrows, pools in beds of drying streams, and similar locations. Sunlight appears to be favorable to larval development, and the absence of vegetation and open shallow water are preferred. It is rarely taken in artificial containers. In Brazil where it gained a foothold (now exterminated) in 1930 the preferred breeding places were in "small, shallow, sunlit pools of fresh water without vegetation" and in the neighborhood of human habitations. Though the above statement is in accord with investigations in many parts of Africa and Brazil, yet Haddow *et al.* (1947) report this species as the most abundant in a tropical rain forest far from human habitation in Bwamba County, Uganda. They took it in the center of the forest and at all elevations from the ground to the tree canopy (82 feet) during both the dry and rainy seasons. Out of a total of 32,315 mosquitoes taken, 30,240 were *A. gambiae.* These captures represent 24 hours of collecting at all levels for 20 days each during 1944 and 1945 in both dry and rainy seasons. (In all 40 collections from both dry and rainy seasons were made in these two years; the elevation stations were at 0, 16, 31, and 54 feet during the rainy season of 1944 and the dry season of 1945 at Mongiro; elevations of 0, 22, 44, 58, and 82 feet were employed during the rainy season of 1944 and the dry season of 1945 at Mamirimiri.)

The *Anopheles maculipennis* complex of Europe and Asia has been studied more intensively than any other anopheline group. Formerly the group was considered a single species with a wide distribution extending from England and Sweden across Russia to Japan and south to coastal areas of northwest Africa and thence east along the northern Mediterranean lands east through parts of Russia to Mongolia. As this species was a good vector of malaria, it became apparent that malaria, even in the centers where it should occur, was absent despite the abundance of this species. Furthermore, it was demonstrated that in some areas the females avoided man and preferred animal hosts (i.e., were zoophilic). The differentiation of the varieties of this complex has involved prolonged studies, and even today the only satisfactory characters are found in the eggs. As a result this complex has been divided into a number of species and subspecies which, even at present, are not well understood. The latest summary of Bates (1940) lists five species and two subspecies. These are *A. maculipennis* Meig., the typical form widely distributed in Europe and probably Asia; *A. messae* Falleroni, closely associated with *A. maculipennis* and with a similar range; *A. melanoon melanoon* Hackett, said to be restricted to the Italian peninsula; *A. melanoon subalpinus* Hackett and Lewis, occurs in Spain, northern Italy, and the Balkans; *A. labranchiae labranchiae* Falleroni, said to be restricted to Spain, Italy, certain Mediterranean islands, and North Africa; *A. labranchiae atroparvus* van Thiel, which is widely distributed in central Europe and Asia; and *A. sacha-*

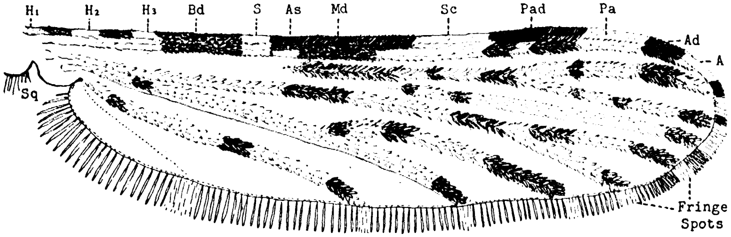

Fig. 131. Wing of *Anopheles gambiae,* illustrating the costal wing spots. *Pale spots:* A, apical spot; As, accessory sector spot; H_1, H_2, H_3, humeral spots; Pa, preapical spot; S, sectoral spot; Sc, subcostal spot. *Dark spots:* Ad, apical dark spot; Bd, basal dark spot; Md, median dark spot; Pad, preapical dark spot; Sq, the squama.

rovi Favr, which is widely distributed in the Mediterranean area east to central Russia and beyond. The biology and the relation of these forms to the transmission of malaria have been fully presented by Hackett and Missiroli (1935) and Hackett (1937).

The subgenus *Myzomyia* Blanchard is known only from the Ethiopian, Oriental, and Australasian regions. The main differentiating character for this group is in the male genitalia. The sidepiece lacks an internal spine and the basal spines number four to six and are not set on tubercles. The wings are nearly always spotted with four pale spots on the costal margin. In the larvae the only character of value is the antennal hair (#11); it is always simple. Here belong a large number of species of which a considerable number are important vectors of malaria. These include *A.* (*M.*) *funestus* Giles (important vector in tropical Africa and Mauritius; *A.* (*M.*) *gambiae* Giles (see above); *A.* (*M.*) *hargreavesi* Evans (vector in Sierra Leone, Nigeria, Belgian Congo, etc.); *A.* (*M.*) *mouchete* Evans (vector in central Africa); *A.* (*M.*) *pharoensis* Theo. (vector in Africa including Egypt, Palestine); *A.* (*M.*) *nili* Theo. (vector in many parts of Africa); *A.* (*M.*) *pretoriensis* Theo. (probable vector when abundant in Africa) and many others as may be seen in Table 7 (pp. 342–347).

DISPERSION AND FLIGHT

"Dispersion" may be differentiated from general "flight" and defined as the ordinary distance mosquitoes travel from their place of breeding to a readily available blood source within a comparatively short distance. "Flight" may be assigned to the conditions when mosquitoes breeding in certain areas have to search for blood at considerable distances such as nearly a mile or more. When food is readily available there may be no need for extended flight; when food is scarce and maximum production of adults occurs, then the adults must go far afield.

Dispersion is undoubtedly the most important question from the standpoint of the epidemiology of the diseases transmitted by mosquitoes, though extended flight must always be taken into account when mass production of any species occurs. In general, it has been fairly well established that a mile zone about the breeding grounds of anophelines is their normal range. However, many factors may intervene to extend this zone, and then we may speak of the "flight" of anophelines or of their distribution. Some of these factors are: (1) mass production in any area in which a blood source is not sufficient to meet the needs of the adults; (2) favoring winds that aid in a wider distribution; and (3) artificial means of distribution that may carry them far beyond any normal flight range. During the past years many experiments have been conducted by mass liberation at central points of anophelines marked by means of aqueous aniline dyes or colored powders such as bronzing, gold, or aluminum powders, etc. After liberation the problem of capture of the marked specimens involves tedious labors and requires a large number of collecting points around the periphery. However, many such experiments have been conducted. Only a brief summary of flight range can be presented here.

FLIGHT RANGE OF ANOPHELINES

Anopheles quadrimaculatus Say has been experimented with by many workers. It seems now fairly well established that a mile zone about its breeding places is the normal, effective dispersal area. However, adults have been taken at 2 to 2.5 miles (3200 to 4000 meters) from the center of liberation (Eyles and Bishop, 1943). Eyles *et al.* (1945) report good dispersal at 2.7 miles and further flights to 3.63 miles, and Gartrell and Orgain (1946) found at Kentucky Reservoir a good 3-mile flight during mass breeding. Huffaker and Back (1945) report similar conditions in Delaware, where mass production occurred over an extensive area (1500 acres of breeding area) and despite abundance of blood supply the females easily migrated to the 1-mile (250 ♀♀ per shed) and to the 1.5-mile (10 ♀♀ per shed) zones. They also report taking females at 3 miles from the breeding zones. Clarke (1943) stained masses of emerging mosquitoes and recovered this species 8 miles distant on the second day and *A. punctipennis* 10.5 miles distant on the seventh day. These studies indicate the maximum ranges recorded for this species, though all workers agree that the effective flight range is a mile or less.

Anopheles crucians Wied. is on record for rather long sustained flights. Metz (1918) noted flights of nearly 2 miles. Barber *et al.* (1924) records extensive flights into Gulfport, Mississippi, from offshore islands where breeding was intensive and no mosquitoes could be found breeding on the coast; the distance varied from 3 to 12 miles. McCreary and Stearns (1937) captured adults at lighthouses in Delaware Bay at 3.2 and 5.5 miles distant from the nearest shore line.

Anopheles freeborni Aitken was noted by Freeborn (1921, 1932) to undertake long migratory flights when emerging from hibernation. The extent was not given but a flight of nearly 4 miles was implied. However there does not seem to be any very definite data on the ordinary dispersal flights during summer breeding.

Anopheles albimanus Wied. has rather extensive flight records. Normally most of the workers stress the usual flight as ½ to 1 mile. These flights occur at dusk and dawn and usually last for 30 to 45 minutes, the dusk flight in search of food and the dawn flight a return to the resting places. However, this species will remain in houses during the day. When mass breeding occurs as on Gatun Lake when it is overgrown with *Naja* and other aquatic vegetation, flights of 12 miles are noted and along with these migrations to the sanitated areas a rise in the malaria rates.

Anopheles gambiae Giles has a flight range of normally ½ to 1 mile, though experiments in various parts of Africa show a maximum range of 4.25 miles down wind and 1.5 miles against wind (Adams, 1940). Haddow *et al.* (1947) found this mosquito the most abundant species in a forested area in Uganda, and it was taken at all flight stations from the ground up to 82 feet in the forest canopy. This would certainly indicate that under favorable conditions this species could migrate long distances. However, in the eradication of this species in northeast Brazil every indication points to localized spread: distant points become infested as the result of various means of carriage. Furthermore, it was found to be almost completely restricted to places surrounding human habitation and never reported from forested areas. In other words it was a house-frequenting, anthropophilic mosquito.

Anopheles maculipennis complex presents a more complicated problem in determining range of dispersion or flight. Extensive flight studies in various parts of Europe by means of released, stained mosquitoes clearly show a flight range of several miles (3 to 4 miles), but which species of this complex is not clearly indicated. In Holland Swellengrebel and Nykamp (1934) found a maximum range of 5.7 to 8.7 miles of marked mosquitoes (♂ and ♀) from their breeding grounds. Shipova (1936) released 1253 stained adults in October and recovered 52 stained individuals in hibernating quarters at 2, 6, 9, and 11.25 miles from the point of release. Many other experiments could be cited but it seems fairly well established that the normal dispersion is usually within the 1- to 2-mile effective range, though longer flights are common and must be taken into consideration when developing effective control measures. *A. sacharovi* Favr, a closely related species, has a recorded range of 2.8 miles (Kligler, 1924) and a maximum seasonal flight of 8.71 miles (Kligler and Mer, 1930).

The flight range of a considerable number of anophelines, particularly those known to transmit malaria, has been investigated. *A. maculatus* Theo., though usually given as rarely dispersing more than a half-mile in Malaya, has been shown by Wallace (1940) and Strahan (1941) to exceed even a mile flight and is an important agent in maintaining malaria to much more than the half-mile zone. *Anopheles minimus* Theo. seems to be restricted to about a half-mile dispersion though longer flights have been recorded (8 miles; Manson and Ramsay, 1933), but such flights do not seem to have been substantiated by other workers. *A. minimus flavirostris* (Ludlow), an important vector of malaria in the Philippines, was shown by Russell and Santiago (1934) to remain rather close to its breeding grounds, rarely exceeding a mile, though previous epidemiological evidence (Craig, 1909) indicated a much greater flight range. The following species appear to be largely restricted to the half-mile or mile zone: *A. aconitus* Donitz, *A. argyritarsis* R.-D., *A. culicifacies* Giles, *A. fluviatilis* Giles; the following to a range of over 1 mile: *A. funestus* Giles, *A. multicolor* Camboulin (max. 8 miles), *A. sacharovi* Favr, *A. pseudopunctipennis* Theo., *A. sergenti* Theo., *A. stephensi* Liston, *A. sundaicus* (Rodenwaldt), *A. superpictus* Grassi, and *A. walkeri* Theo. (1.5 to 2 miles).

FLIGHT RANGE OF CULICINES

The dispersion of culicines has not received the same attention as that of anophelines. The following brief notes may be of interest.

Culex pipiens Linn. has been taken at least 14 miles from where the mosquitoes were dusted with aniline dyes (Clarke, 1943) during a period of 47 days, the average flight range being 9.2 miles. McCreary and Stearns (1937) captured a male and females (12) by light traps 8.2 and 8.4 miles from the nearest shore line. Employing marked specimens Afridi *et al.* (1938) reported *Culex fatigans* Wied. infiltrating into the urban areas of Delhi for at least 3 miles. *Culex apicalis* Adams, *C. salinarius* Coq., and *C. restuans* Theo. have been taken at light traps at 8.2, 8.4, and 3.2 miles respectively from the nearest shore line (McCreary and Stearns, 1937).

Aedes aegypti (Linn.) has apparently a narrow range of dispersal. Shannon and Davis (1930) in extensive experiments in Brazil demonstrated a sustained flight over open water of 1000 meters by employing stained specimens. Its dispersal on land is known to exceed 500 yards, but in general its movements are rather closely restricted to human habitations where it migrates from house to house and its nearby breeding grounds from day to day.

Aedes albopictus (Skuse), like *A. aegypti,* has a restricted range of movement. Bonnet and Worcester (1946) in a series of well-planned experiments in

Hawaii with marked individuals concluded that the dispersal range rarely exceeds 200 yards during the lifetime of the adults. *Aedes sollicitans* (Walker) is known to migrate considerable distances by mass flights, at least 30 to 40 miles. Curry (1939) recorded an invasion of a ship 110 miles distant from Cape Henry, North Carolina, by a swarm that caused considerable annoyance to the passengers. In Delaware McCreary and Stearns (1937) collected large numbers of males and females at light traps placed 8.2 and 8.4 miles from the shore line. In the same traps *Aedes cantator* (Coq.) were also taken. Though these two species breed primarily along our tidal marshes, yet they have been taken in many of the salt pools located inland as at Ithaca and Syracuse, New York, and at various points inland in Alabama, Florida, Georgia, North and South Carolina, and Mississippi. *Aedes squamiger* (Coq.) a salt-marsh breeder along the southern half of the California coast line is stated by Herms and Gray to migrate as much as 50 miles. *Aedes taeniorhynchus* (Wied.), another salt-marsh breeder, is known to migrate considerable distances, though verified flights do not exceed eight or nine miles (McCreary and Stearns, 1937). Like *A. sollicitans* it has been found breeding in salt pools far inland (30 to 240 miles) but this is certainly not an invasion by sustained flight. Probably the most extended flights of salt-marsh breeders are by *Aedes vigilax* Skuse, for which Hamlyn-Harris (1933) reports 60-mile migrations in Australia, and *Aedes* (*Mucidus*) *alternans* Westw. 80-mile migrations.

Among fresh-water-breeding mosquitoes there are a number of interest. *Aedes vexans* Meig. has many records of 5-, 10-, and even 20-mile migrations from known breeding grounds, and in many cases the migratory flights have been followed day by day from breeding grounds for at least 5 miles. *Aedes lateralis* (Meig.), a serious pest in British Columbia, Washington, and Oregon, is known to migrate at least 10 to 30 miles. Stained specimens were actually taken 5 miles from the point of liberation, and the species was abundant 15 miles from its breeding grounds but gradually diminished at the 25-mile limit: one was taken 30 miles from breeding grounds (Stage, 1938). *Aedes dorsalis* (Meig.) and *Aedes spencerii* (Theo.) are reported as migrating several miles but no experimental data are available. One female of the latter species was taken at Lake Placid, New York, on July 26, 1945, over at least 500 miles from its known eastern range.

The problem of mosquito dispersion by air currents or flight to the upper reaches of the atmosphere presents another phase. It is now well known that a number of mosquitoes frequent the upper canopy in many tropical forests. The work of Glick (1939) demonstrated that mosquitoes may be collected at quite high levels both day and night during their breeding season. In all, 111 specimens of mosquitoes were taken in airplane flights throughout the five years, representing seven genera and six determined species. Of these, 44 were taken in the daytime and 67 at night. The night flying was only 10 per cent of the total time in the air. *Anopheles quadrimaculatus* was taken both day (3) and at night (8) up to elevations of 1000 feet; five *Culex* species were taken at elevations of 200 and 5000 feet. *Aedes vexans* was taken at night at 500 feet to 5000 feet.

CLASSIFICATION OF THE CULICIDAE

KEYS TO THE SUBFAMILIES, TRIBES, GENERA, AND SUBGENERA

The Subfamilies

ADULTS

Mouth parts not prolonged into a proboscis, extending little beyond the clypeus; scales, when present, largely confined to the hind margin of the wing .... *Chaoborinae* [8]

Mouth parts prolonged into a proboscis, extending far beyond the clypeus; scales always present on the wing veins and along the marginal fringe; legs with scales; body usually with scales or they may be almost absent .... *Culicinae*

LARVAE (4th instar)

Antennae prehensile, with long and strong apical spines (Fig. 94) .... *Chaoborinae* [8]

Antennae not prehensile and lacking the strong apical spines ...... *Culicinae*

PUPAE

1. Swimming paddles fused basally, not movable; with apical and lateral articulated spines or hairs .... (*Corethrella*) *Chaoborinae* [8]
   Swimming paddles free, movable; without long hairs or spines 2
2. Respiratory horn either almost closed apically or with the spiracular opening near the middle; surface of horn with hexagonal reticulations .... *Chaoborinae* [8]
   Respiratory horn open at tip, spiracle at its base .... *Culicinae*

The Tribes of the Culicinae

ADULTS

1. Proboscis rigid; basal half stout, the apical half more slender and bent

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[8] Not further treated here; adults never take blood.

sharply backwards; scutellum evenly rounded with marginal hairs and scales well distributed .... *Megarhinini*

Proboscis not rigid, of nearly uniform thickness (though the apex may be swollen) and the apical half not bent sharply backwards 2

2. Scutellum evenly rounded, crescent-shaped, or it may be slightly lobed (as in *Chagasia*), without or with few scales but the marginal hairs evenly distributed; first tergite of abdomen always without scales; sternites nearly always bare of scales; palpi of males and females as long or nearly as long as proboscis (except in *Bironella*) (Fig. 125) .... *Anophelini*

Scutellum trilobed with the hairs restricted to the lobes; scales nearly always present and usually in patches; abdomen with tergites and sternites clothed with scales; palpi in the females short; in the males long and bushy (Fig. 125) 3

3. Base of hind coxa in line with the upper margin of the meron; (Fig. 99, *8*); postnotum with a group of bristles (all American species); abdomen almost completely free of hairs and usually compressed .... *Sabethini*

Base of hind coxa distinctly below upper margin of meron; postnotum lacking bristles, smooth (except in some oriental species of *Aedes*); abdomen with hairs on hind margins of segments .... *Culicini*

LARVAE (4th instar)

1. Eighth segment without an elongated siphon or respiratory tube, the spiracles sessile .... *Anophelini*

Eighth segment with an elongated siphon or respiratory tube which is at least as long as broad 2

2. Mouth brushes prehensile, each composed of 10 stout rods .. *Megarhinini*

Mouth brushes not or rarely prehensile, each composed of 30 or more hairs 3

3. Anal segment with one pair of ventral hairs or tufts instead of a brush; siphon usually with numerous hairs or tufts .... *Sabethini*

Anal segment with a ventral brush, usually large but at least four separate hairs or tufts; siphon usually with tufts but these in definite arrangement .... *Culicini*

PUPAE

1. Lateral apical hairs of abdominal segments, except the last pair, are blunt spines and placed almost exactly at the corners ..... *Anophelini*

Lateral apical hairs of abdominal segments placed well before the apical corners and each consists of a branching hair or a single hair 2

2. Outer part of paddle produced beyond the tip of midrib .... *Megarhinini*
   Outer part of paddle not longer than midrib 3
3. Seventh and eighth segments with large posterolateral tufts; paddles smooth and lack apical hairs .... *Sabethini*
   Abdomen not as described above; paddles with apical hairs ..... *Culicini*

Genera and Common Subgenera of Tribe Anophelini

ADULTS

1. Scutellum slightly trilobed (South American) .... *Chagasia* Cruz
   Scutellum crescent-shaped, evenly rounded 2
2. Stem of second fork cell wavy .... *Bironella* Theobald
   Stem of second fork cell straight .... *Anopheles* Meigen 3
3. Thorax blackish with a broad gray line from neck to scutellum .... Subgenus *Stethomyia* Theobald
   Thoracic ornamentation quite otherwise 4
4. Wings with rarely more than two pale spots on costa; sidepiece of male genitalia with 1 to 3 (usually 2) strong basal spines set on tubercles .... Subgenus *Anopheles* Meigen
   Wings with 4 or more pale costal spots (Fig. 131) 5
5. Sidepiece of male genitalia with one spine at base and two beyond. (New World species) .... Subgenus *Nyssorhynchus* Blanchard
   Sidepiece of male genitalia with several weak spines near base and not set on tubercles. (Old World species) .... Subgenus *Myzomyia* Blanchard

LARVAE (4th Instar)

1. Body of larva densely clothed with short hairs in addition to the regular hairs; leaflets of palmate tufts greatly expanded apically and each ending in a long central hair. Anterior flap of spiracular apparatus produced into a long, stout, bristlelike structure ...... *Chagasia* Cruz
   Body of larva not densely covered with fine hairs; leaflets of palmate tufts not as described above; no prolongation of anterior flap of spiracular apparatus 2
2. Two pairs of palmate hairs on the thorax .... *Bironella* Theobald
   At most one pair of palmate hairs on thorax .... *Anopheles* Meigen

Key to Genera of the Tribe Culicini: Adults
(Modified from Edwards, 1932)

1. Squama fringed (fringe usually complete); anal vein (6th) reaching well beyond the base of cubital fork (fork of 5th vein) 4

Squama bare (Fig. 131) or with 1 to 4 short hairs; second marginal cell (R_2) shorter than its stem; anal vein (6th) ends about opposite of cubital fork (fork of 5th vein) 2

2. Wing membrane lacks microtrichia; second marginal cell (R_2) shorter than its stem; anal vein (6th) ends about opposite the base of fork of 5th vein .... *Uranotaenia* Lyn. Arrib.

Wing membrane with distinct microtrichia 3

3. Second marginal (R_2) cell shorter than its stem; several posterior pronotal bristles; wing scales not emarginate at tips. (One species, Malaya) .... *Zeugnomyia* Leicest.

Second marginal cell longer than its stem; 2 posterior pronotal bristles; wing scales emarginate at tips. (Africa, India, S. Pacific) .... *Hodgesia* Theobald

4. Pulvilli present; pleural chaetotaxy well developed but spiracular and postspiracular bristles absent 5

Pulvilli absent or rudimentary; spiracular and postspiracular bristles present or absent or one set may be present 6

5. Antennae much longer than the proboscis; first flagellar segment of antenna as long as several of the following segments taken together; antennae similar in both sexes, never very bushy. (Sea coasts of the Gulf, Caribbean, and West Indies) .... *Deinocerites* Theobald

Antennae not much longer than the proboscis; first flagellar segment not as long as several of the following segments taken together; male antennae very bushy and different from the female. (World-wide in distribution) .... *Culex* Linnaeus

6. Postspiracular bristles absent; claws of female generally simple (except in species of *Haemagogus*) 7

Postspiracular bristles present (at times only 1 or 2); claws of female usually toothed; dorsocentrals and upper sternopleurals nearly always well developed 13

7. Spiracular bristles present (at times only 1 or 2) .... *Culiseta* Theobald

Spiracular bristles absent 8

8. Pronotal lobes almost touching dorsally; dorsocentral and prescutellar bristles absent .... *Haemagogus* Williston

Pronotal lobes well separated; dorsocentral and prescutellar bristles well developed. 9

9. Postspiracular area with scales; claws of female usually toothed; palpi of female more than half as long as proboscis ..... *Armigeres* Theobald

Postspiracular area bare; claws of female simple; palpi of female not half as long as proboscis 10

10. All segments of female antennae and last two of male antennae short and thick; middle femur with a scale tuft ...... *Aedomyia* Theobald

Antennae slender; middle femur without a scale tuft 11

11. First segment of front tarsus longer than the last four taken together; 4th segment very short, only as long as wide; mesonotum usually with narrow longitudinal lines of silvery-white scales .... *Orthopodomyia* Theobald

First segment of front tarsus not so long, or as long, as the last four taken together; 4th segment not as described above 12

12. Proboscis of male much swollen apically; of female slightly swollen or else cell R_2 (2nd marginal) shorter than its stem .... *Ficalbia* Theobald

Proboscis of male or female not swollen apically; cell R_2 (2nd marginal) as long as its stem .... (in part) *Mansonia* Blanchard

13. Spiracular bristles present, at times only 1 or 2. (The Americas) .... *Psorophora* Rb.-Desvoidy

Spiracular bristles absent 14

14. Eyes widely separated; space between and back of the eyes with metallic silvery scales (African) .... *Eretmapodites* Theobald

Eyes not so widely separated, almost touching; space between and back of the eyes not clothed with metallic silvery scales 15

15. Wing scales mostly narrow (when broad the female claws are toothed) 16

Wing scales all very broad; female claws not toothed .... (in part) *Mansonia* Blanchard

16. Proboscis slender, not recurved at tip in repose; ornamentation varied .... *Aedes* Meigen

Proboscis stout, recurved at tip in repose; dark species with flat scales on vertex and scutellum .... *Armigeres* Theobald

LARVAE (4th instar)

1. Distal half of air tube (siphon) sharply attenuated and apical portion provided with sawlike teeth for penetrating plants .... *Mansonia* Blanchard

Air tube (siphon) not as described above 2

2. Head longer than broad or as long as broad (appearing more or less as rounded); 8th abdominal segment with a lateral chitinous plate with one row of comblike teeth on its posterior margin; antennae not inflated or very large .... *Uranotaenia* Lyn. Arrib.

Head always broader than long; 8th abdominal segment without such a plate (except at times in certain *Psorophora* and all *Aedomyia* spp. but in these the antennae are inflated and flattened) 3

3. Air tube with pecten; the teeth of the pecten nearly always denticulate 4

Air tube without pecten or rarely a few simple teeth and these not denticulate 9

4. Air tube with several pairs of ventral hair tufts (never less than 2 pairs) and occasionally scattered dorsal hairs or the air tube is extremely long and slender with hair tufts apparently lacking 5

Air tube not as described above; with never more than a single pair of hair tufts or in addition there may be a median ventral line of hair tufts 7

5. Mouth brushes prehensile, often appearing as matted tufts or as rods .... (Subgenus *Lutzia*) *Culex* Linnaeus

Mouth brushes normal, composed of long hairs 6

6. Head with a prominent pouch on each side enclosing the mandible, which has a hairy base .... *Deinocerites* Theobald

Head not as described above; mandibles without a hairy base .... *Culex* Linnaeus

7. Air tube with a pair of basal hair tufts only or a pair of basal hairs (single) .... *Culiseta* Felt

or

Air tube with a pair of basal hair tufts and a median row of ventral tufts .... (Subgenus *Climacura*) *Culiseta* Felt

Air tube with a single pair of ventral tufts placed near the middle of tube or beyond; if tufts are lacking or vestigial the anal segment is completely ringed by the dorsal plate or saddle and pierced by some of the tufts of the ventral brush 8

8. Anal segment completely ringed by the saddle; the saddle is pierced on the mid-ventral line by tufts of the ventral brush; air tube often swollen and pecten of few teeth .... *Psorophora* Rb.-Desvoidy

Anal segment not completely ringed by the saddle, but, if so, the ventral brush is confined posterior to the ring (no tufts pierce the saddle) .... *Aedes* Meigen
.... *Haemagogus* Williston

9. Antenna short with a simple hair on shaft; antenna more or less cylindrical, never inflated 10
   Antenna longer with a branched hair on shaft; antenna may be cylindrical or inflated or flattened 12
10. Ventral tuft of air tube large 11
   Ventral tuft small and simple. (Only 1 species, from Malaya) .... *Zeugnomyia* Leicester
11. Ventral brush of anal segment well developed with a barred area. (Oriental and Australasian) .... *Armigeres* Theobald
   Ventral brush of anal segment with never more than four pairs of single hairs, usually 1 or 2 pairs of branched hairs; they never form a barred area. (African) .... *Eretmapodites* Theobald
12. Antenna very large, flattened, not cylindrical in cross section. (South and Central America, Africa, and Oriental region) .... *Aedomyia* Theobald
   Antenna never very large and flattened, usually cylindrical in cross section 13
13. Large sclerotized plates present on dorsum of abdominal segments 6 to 8 or rarely absent .... *Orthopodomyia* Theobald
   Sclerotized plates absent on abdominal segments 6 to 8 14
14. Hair tuft of antenna well removed from apex; anal segment ringed by saddle .... *Ficalbia* Theobald
   Hair tuft of antenna close to apex; anal segment ringed by saddle ... . *Hodgesia* Theobald
   Hair tuft of antenna before the middle; anal segment not ringed by the saddle or dorsal plate .... *Orthopodomyia* Theobald

It is not feasible to offer keys to species of mosquitoes, even the anophelines (except those of North America), in a limited textbook. The student is referred to the bibliography where he will find references (and references with extended bibliographies are double-starred) which will enable him to locate keys to the species of nearly any region of the world. In addition to keys he must have detailed descriptions and a wealth of illustrations.

KEY TO THE ANOPHELINES OF NORTH AMERICA

Adults (Males and Females)

1. Hind tarsus with apical portion of second and all of third and fourth segments white; fifth segment white with a narrow, basal, black ring .... (Subgenus, *Nyssorrhynchus*) *albimanus* Wied.

Tarsal segments of all legs dark or black without white markings . . . . . . (Subgenus, *Anopheles*) 2

2. Scales of the wings entirely dark or black; apex of wing may have a single coppery or light spot 3

Wings with distinct spots or areas of white or light-colored scales on the veins as well as on the costal margin 9

3. Scales of the wings not grouped in spots but evenly distributed on the veins; legs and palpi dark-scaled. A small species that breeds in tree holes . . . . . . *barberi* Coq.

Scales of the wings grouped in darker spots which are usually very distinct; palpi may be dark-scaled or ringed with white 4

4. Segments of the palpus with narrow white rings at their apices; terminal segment with white apex; white or yellowish knee spots (apices of femora) present; wing spots usually distinct . . . . . . *walkeri* Theo.

Palpi entirely dark-scaled, rarely any pale scales present 5

5. Wing spots usually not very distinct; knee spots absent; general coloration very dark . . . . . . *atropos* D. & K.

Wing spots very distinct; knee spots present; general coloration not so dark 6

6. Apex of wing with a distinct coppery or golden patch of scales; mesonotum with a broad, median, longitudinal, whitish (pruinose) stripe 7

Apex of wing without such a spot, uniformly dark 8

7. Wing 5 to 6 mm. in length; stem vein of second longitudinal vein beyond dark spot with outstanding scales . . . . . . *earlei* Vargas

Wing rarely more than 5 mm. in length, frequently less; stem vein of second longitudinal vein beyond dark spot with closely appressed scales, none outstanding . . . . . . *occidentalis* D. & K.

8. Mesonotum uniformly colored, no distinct stripe; occurs east of the Rocky Mountains and is widely distributed from Canada to the Gulf of Mexico . . . . . . *quadrimaculatus* Say

Mesonotum with a pale pruinose stripe, fading out anteriorly; occurs in the Rocky Mountain region and west of it; the dark spots of the wings are usually more dense . . . . . . *freeborni* Aitken

9. Costal margin dark except a white or yellowish-white spot at extreme apex of wing; vein 6 with three dark spots separated by white scales.

Stem of 5th vein dark-scaled . . . . . . *crucians* Wied.

. . . . . . *georgianus* King

Stem of 5th vein all white-scaled . . . . . . *bradleyi* King

Costal margin of wing with 2 white spots, one near apex and a large one at outer third near apex of subcostal vein; vein 6 with only 1 or 2 dark spots 10

10. Veins 3 and 5 dark-scaled; vein 6 with short basal black spot separated by a light area from the dark apical half; wing fringe without pale spots at tips of veins; palpus black .... *punctipennis* Say

Veins 3 and 5 with central areas largely pale-scaled; vein 6 with basal half white, apical half black; wing fringe with pale spots at tips of veins 11

11. Terminal segment of palpus entirely white; vein 4 pale before fork .. .. *pseudopunctipennis* Theo.

Terminal segment of palpus white at base, apical half black; vein 4 black before the fork .... *franciscanus* McC.

Males (Based on the Genitalia)

1. Sidepiece with 4 stout spines—1 basal, 2 accessory, and 1 internal (Subgenus *Nyssorhynchus*) .... *albimanus* Wied.

Sidepiece with 3 stout spines—2 basal, 1 internal. (Subgenus *Anopheles*) 2

2. Mesosome without leaflets 3

Mesosome with leaflets 4

3. Dorsal lobe of claspette nearly cylindrical in shape with 3 apical, closely appressed, overlapping spines, the outer 2 sharply curved at tips and forming a kind of hood; these spines nearly twice as long as the lobe .... *barberi* Coq.

Dorsal lobe of claspette as above but with 3 apical, bladelike spines, all about the same length and size; spines not as long as the lobe .... *franciscanus* McC.

4. Leaflets of mesosome deeply serrate, varying from 2 to 4 pairs and difficult to see .... *pseudopunctipennis* Theo.

Leaflets of mesosome not serrate 5

5. Sidepiece with numerous scales; dorsal and ventral lobes of each claspette fused to form a conical lobe; this lobe bears 5 spines, rarely less; lobes of ninth tergite very long and pointed .... *crucians* Wied.
.... *bradleyi* King
.... *georgianus* King

Sidepiece without scales or, rarely, a few present; dorsal and ventral lobes of claspette distinct; lobes of ninth tergite usually not so long or so pointed 6

6. Dorsal lobe of claspette with bluntly rounded apical spines, sometimes expanded at apices or partially fused 7
Dorsal lobes of claspette with pointed spines 9

7. Lobes of ninth tergite short, stout, usually expanded at apices; spines of dorsal lobe of claspette not expanded at apices but generally more or less fused and rounded .... *quadrimaculatus* Say
Lobes of ninth tergite long and pointed or slightly rounded; spines of dorsal lobe of claspette not as described above 8

8. Dorsal lobe of claspette with 2 spines fused at their bases and each terminating in an enlarged and rounded knob; ventral lobe with only 2 rather large, pointed spines; apical leaflet of mesosome not twice as long as the second leaflet .... *walkeri* Theo.
Dorsal lobe of claspette with 2 spines, each terminating in a rounded knob but each spine arises from a separate tubercle and they are not fused at their bases; apical leaflet of mesosome twice as long as the second leaflet .... *atropos* D. & K.

9. Dorsal lobe of claspette with 2 sharply pointed, apical spines, the spines so closely associated as to appear as only one; ventral lobe of claspette with a large, pointed apical spine, a smaller internal spine, and a minute spine between them; lobes of ninth tergite short, stout, and slightly expanded apically .... *punctipennis* Say
Lobes of claspette not as described above; lobes of the ninth tergite long or short, but if short, pointed apically or expanded 10

10. Dorsal lobe of claspette with 2 or 3 sharply pointed spines, the spines so closely associated as to appear almost as one; lobes of the ninth tergite long, narrow, and rounded apically .... *freeborni* Aitken
Dorsal lobe of claspette similar to that described above; lobes of ninth tergite short, broad, and expanded at apex .... *earlei* Vargas
Dorsal lobe of claspette similar to that described above; lobes of ninth tergite somewhat longer, narrow, and rarely expanded at apex .... *occidentalis* D. & K.

Larvae (*Fourth Instar*)

1. Abdomen with plumose, lateral hairs on the first six segments; all head hairs small, single. Larvae occur in tree holes .... *barberi* Coq.
Abdomen with plumose, lateral hairs on the first three segments only; frontal hairs (Nos. 5, 6, and 7) large and plumose 2

2. Palmate hairs well developed on abdominal segments 1 to 7; both inner

and outer clypeal hairs long and slender; inner clypeal hairs widely separated and feathered on outer half; outer clypeal hairs with minute branches on the outer half .... *albimanus* Wied.

Palmate hairs well developed on abdominal segments 2 or 3 to 7; inner and outer clypeal hairs not as described above 3

3. Outer clypeal hairs not densely branched dichotomously 4

Outer clypeal hairs densely branched dichotomously 6

4. Inner, outer, and posterior clypeal hairs long, single, subequal, and widely separated at their bases 5

Inner and outer clypeal hairs long, usually with 1 to 5 branches near the tips; posterior clypeal hairs short and may be branched; inner clypeal hairs are closely approximated at their bases .... *atropos* D. & K.

5. Inner angle of each posterior plate of respiratory apparatus produced into a long, sclerotized tail. (In living larvae these tails are bent upward at right angles to the plate and project through the water) .... *pseudopunctipennis* Theo.

Inner angle of each posterior plate rounded and not produced into a tail .... *franciscanus* McC.

6. Abdominal segments 4 and 5 with 2 conspicuous hair tufts (Nos. 2 and 0) anterior to the palmate tuft; these tufts are approximately equal in size and have 4 to 9 branches .... *crucians* Wied.

Abdominal segments 4 and 5 with only 1 hair tuft (No. 2) anterior to each palmate tuft; hair 0 vestigial or lacking, or, if present, the inner clypeal hairs are sparsely feathered toward the tips 7

7. Inner clypeal hairs divided into 2 or 3 branches or feathered toward the tips 8

Inner clypeal hairs unbranched (rarely divided into 2 branches near the middle) 9

8. Inner clypeal hairs closely approximate, so close that an extra tubercle of the same size cannot be placed between their bases; each clypeal hair is sparsely feathered on the apical half; occipital hairs (Nos. 8 and 9) small, each with 2 to 4 branches .... *walkeri* Theo.

Inner clypeal hairs not so closely placed that an extra tubercle of the same size cannot be inserted between their bases; inner clypeal hairs with 2 or 3 branches near the middle; occipital hairs with many branches and stout shafts .... *earlei* Vargas

9. Inner clypeal hairs separated at their bases by at least the diameter of one tubercle; palmate tufts well developed on segments 3 to 7; palmate tuft on segment 2 frequently well developed; occipital hairs well

developed with 8 to 10 branches .... *quadrimaculatus* Say
.... *occidentalis* D. & K.

Inner clypeal hairs so closely placed that an extra tubercle cannot be inserted between their bases 10

10. Palmate tufts present only on segments 4 to 6 .... *georgianus* King
Palmate tufts present on segments 3 to 7 11

11. Palmate tufts on segments 3 and 7 smaller than the others; inner clypeal hairs normally placed close together .... *bradleyi* King
Palmate tufts on segments 3 and 7 of the same size as the others 12

12. Hair No. 2 on abdominal segments 4 and 5 multiple (4- to 5-branched) .... *freeborni* Aitken
Hair No. 2 on segments 4 and 5 single .... *punctipennis* Say

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CHAPTER XI

Mosquitoes in Relation to Human Welfare

MOSQUITOES have always plagued man and animals. They have limited and still limit man's occupation of many regions of the globe. Always considered as abominable pests about which he knew little and cared less, he was suddenly awakened to their extreme importance by the discovery by Ronald Ross, in 1898, that they are the transmitters of malaria or ague. Long before this, in 1878–1879, Patrick Manson had shown that mosquitoes were the intermediate hosts of *Wuchereria* (*Filaria*) *bancrofti,* a roundworm that causes serious diseases of man. This discovery had not attracted much notice as the diseases caused by this worm were not known and even yet are not well understood. The incrimination of *Aedes aegypti* (the tiger mosquito) as a vector of yellow fever by Dr. Carlos Finlay (1881–1900) and the final proof in 1900 by Reed, Carroll, Lazear, and Agramonte aroused the greatest interest in the mosquito problem. At present, mosquitoes are regarded as probably the most important group of all our bloodsucking insects. In general, mosquitoes may be said to affect human welfare in the following ways:

1. Direct irritation caused by their bites.
2. Diseases of man which are transmitted through the agency of mosquitoes.
3. Diseases of domestic and game animals which are transmitted by mosquitoes.
4. Reduction in land, real estate, and other property values, due to the excessive abundance of mosquitoes.

DIRECT IRRITATION

To many persons the bites of mosquitoes are only a temporary annoyance; some do not notice their bites; but many people suffer greatly even from a few bites. The number of people who appear almost immune to mosquito attacks is probably not large, and this immunity may be confined to the bites of mosquitoes present in their region. Other species of mosquitoes may cause them great annoyance. As this phase of the mosquito problem has never been sufficiently stressed, I desire to call particular attention to it, especially at this time when so much emphasis is placed on living out of doors to conserve our health. Mosquitoes probably affect young children, particularly babies, more than we know. To many people the bites are very severe, causing swellings and severe itching, followed by incessant scratching and the formation of pustules. This is followed by restlessness, loss of sleep, nervous irritation, and a determination to avoid mosquito areas at all costs. In many persons the lesions caused by mosquito bites remain for months and retain an itching sensation. Frequently mosquito outbreaks may assume such proportions that all outdoor work has to be abandoned, and when this occurs year after year the development of the district is greatly retarded if not entirely abandoned. Bishopp (1933) reported the deaths of 173 head of livestock in Florida due to attacks of *Psorophora confinnis,* and the milk supply of the area was reduced 1000 gallons per day. When mosquitoes are abundant, domestic animals suffer, especially during the evening and night hours. In housed animals such attacks may be greatly reduced by the use of DDT (see pp. 389-391).

DISEASES TRANSMITTED BY MOSQUITOES

At least thirteen important human diseases of wide distribution are transmitted by mosquitoes and in most cases only by mosquitoes. If the transmitting mosquitoes could be eliminated, the diseases would largely disappear. These are malaria (four kinds), yellow fever, dengue, filariasis (two), encephalitis (at least four different diseases), and Rift Valley fever.

MALARIA

Malaria, according to Boyd (1930), is the worst scourge of mankind. The disease is caused by a minute protozoan that invades the red corpuscles (Figs. 132,133). There are known to be four distinct species of malarial parasites, and each produce a distinct type of disease. The parasites are known as *Plasmodium vivax* (Fig. 132), causative agent of benign tertian or vivax malaria; *Plasmodium malariae,* causative agent of quartan malaria; *Plasmodium falciparum,* the agent of malignant, subtertian, pernicious, or aestivo-autumnal malaria; and *P. ovale,* the causative agent of ovale malaria. The common and most prevalent type of malaria in North America is the tertian.

Pernicious or aestivo-autumnal malaria occurs in the states bordering on the Gulf of Mexico. According to Hoffman (1916), the prevalence of the various types of malaria in the southern states is about 65 per cent for tertian, 13 per cent for quartan, and 22 per cent for aestivo-autumnal. Malaria is one of the most widely distributed of human diseases. It occurs in most of the great fertile regions of the earth; its present distribution and extent of endemicity is shown in Fig. 134.

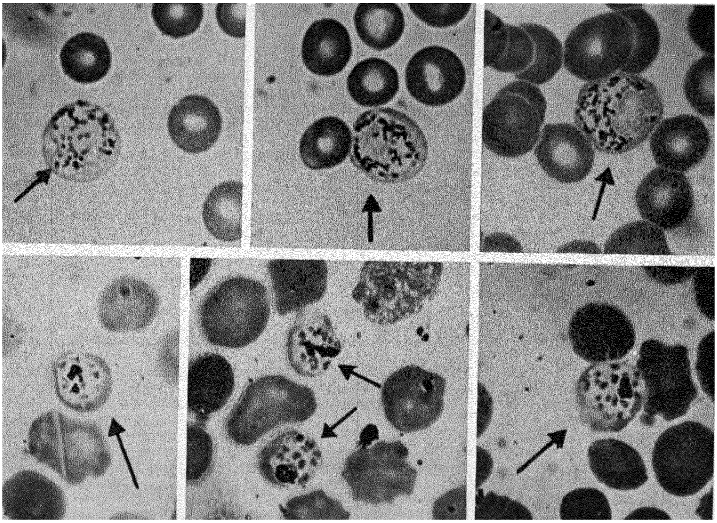

Fig. 132. Malaria parasites in human blood. *Upper row: Plasmodium vivax* in various stages in the formation of merozoites. *Lower row: Plasmodium falciparum* in placental blood, showing the formation of merozoites and the marked dot of pigment. Note that in *P. vivax* the red cells are greatly enlarged while in *P. falciparum* there is no apparent enlargement of the red cells. (Photographs by the author.)

In order to understand the essential role played by anopheline mosquitoes in the transmission of malaria, a very brief outline of the life cycle of *Plasmodium vivax* is here presented. *Plasmodium vivax,* in man, lives and multiplies asexually in the red blood corpuscles (Fig. 132). This is known as the asexual cycle (the human or intrinsic phase). As the parasites grow (Fig. 133 1–3) they cause the red cells to become enlarged (not true of *Plasmodium falciparum*) and absorb the cell contents. At the end of about 40 hours, the trophozoite is mature and is now called a schizont (5). During the next eight

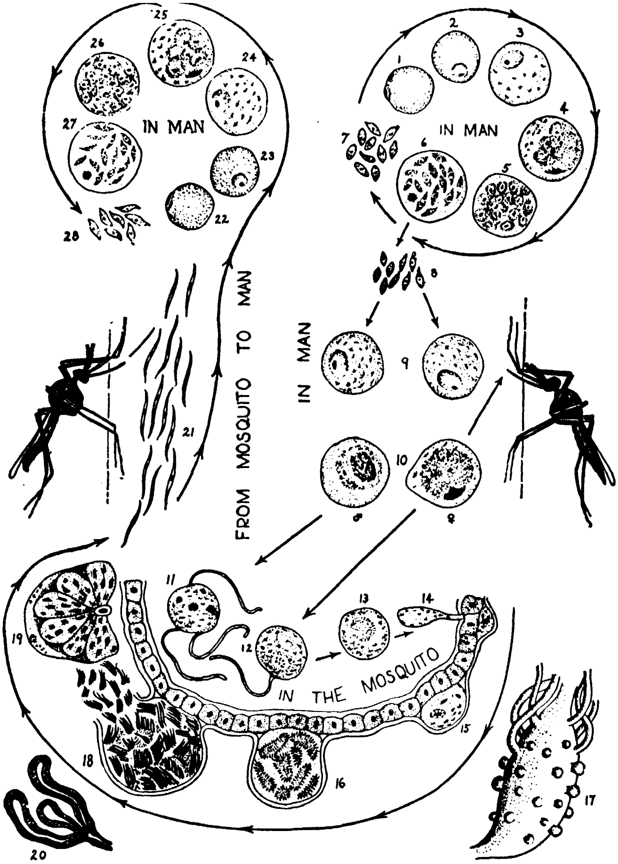

Fig. 133. Diagrammatic representation of the life cycle of the benign tertian malaria parasite (*Plasmodium vivax*) in man and the mosquito. Nos. 1 to 4 show the growth of the parasite in the red blood cells; 5 and 6, the mature schizont dividing into merozoites, and their escape is shown in 7; these merozoites invade new red cells and the cycle continues. Nos. 8, 9, and 10 show the development of the male and female gametocytes. The mosquito is shown obtaining these sex cells. No. 11, the male cells (sperm) being discharged; 12, the sperm cell uniting with the female cell; 13, the fertilized zygote; 14, the migrating egg or ookinete; 15, the oocyst outside the stomach wall of the mosquito; 16, a nearly mature oocyst; 17, the stomach of a mosquito showing oocysts; 18, the discharge of the sporozoites by the breaking of the oocyst; 19, sporozoites in the salivary gland; 20, the salivary glands of a mosquito; 21, an anopheline is seen discharging sporozoites into the blood stream of a new host; 22 to 28 show the asexual cycle in a new host. (Modified from James.)

hours each schizont divides into a number, 12 to 24, merozoites and these are discharged into the blood stream by the rupturing of the cell wall (6 and 7). Along with the merozoites are liberated the wastes, pigments, and probably a toxin. Each merozoite now attacks a new red cell and, in about 40 hours, becomes a schizont, which divides, and liberates the merozoites at the end of about 48 hours. The escape of so many merozoites with their wastes corresponds with the onset of a chill followed by a marked rise in the temperature of the patient. Hence this type is known as the tertian or three-day fever, the chill and fever appearing on the third day. After the asexual cycle has continued for a number of days, there appears a new stage in the cycle of the parasite. Certain merozoites develop into male and female gametocytes or sex cells (8, 9, and 10). Two kinds are produced, male or microgametocytes and female or macrogametocytes. These now remain in the red blood cells and no further development takes place.

At this point the anopheline mosquito becomes essential for the continuance of the life of the parasite. If a person having the micro- and macrogametocytes in his blood is bitten by a suitable anopheline mosquito (as *Anopheles quadrimaculatus*) and numbers of these sex cells are obtained, a further remarkable development takes place in the stomach of the mosquito. The female or macrogametocyte matures into what is called a macrogamete and is then ready for fertilization. The male cell or microgametocyte gives off a number of small linear bodies, which are the true microgametes or male elements (11). These lash about till they find a macrogamete and one of them immediately penetrates it (12) and completes the process of fertilization. The union of the male and female produces a zygote (13). The zygotes are produced in the stomach of the mosquito. The zygote, at first passive, soon elongates and begins active movement; hence it is called the ookinete (14). The ookinete penetrates the wall of the stomach and establishes itself between the epithelial and muscular layers (15). Here it becomes spherical and grows very large by the absorption of food from the surrounding tissues. It is now called an oocyst (16). Within the oocyst remarkable changes (sporogony) take place and, at the end of four or five days, the oocyst is completely filled by very minute organisms, the sporozoites (18). The sporozoites escape by the bursting of the oocyst and are freed in the body cavity. As insects have no closed circulatory system, the blood bathing all the tissues, the sporozoites are now free to wander with the blood. They are said to bore into almost all the tissues and organs of the host, but great numbers of them invade the salivary glands (19). The sporozoites are now ready to be passed with the salivary secretion into a new host when the mosquito bites (21). The entire cycle (called the exogenous or extrinsic phase) within the mosquito occupies from 8 to 14 days or longer, depending on the temperature and other factors. It will thus be seen that the presence of anopheline mosquitoes is essential for the beginning of a new infection in man and furthermore that man with gametocytes in his blood is essential before mosquitoes can become infected. This interdependence, the so-called etiological chain of malaria, is well shown in Fig. 133. If this chain can be broken at any one point, a reduction or even a complete elimination of the disease can be accomplished.

In the above account it would appear that the sporozoites discharged by the infected mosquito into the blood stream of a susceptible person invade the red cells directly and start the malaria cycle. This view has been generally held though the work on bird malarias has shown that such is not the case in those species causing diseases in birds. No observer has ever seen the direct invasion of red cells by sporozoites of human malarias. Shortt and Garnham (1948) have demonstrated that in monkey malaria (*Plasmodium cynomolgi*) and human malaria (*Plasmodium vivax*) the sporozoites undergo a cyclical development in the parenchymatous cells of the liver. In *P. vivax* the sporozoites invade the liver cells and each sporozoite grows into an ovoid mass, forming a cyst.[1] Within each cyst the chromatic material (nucleus?) divides repeatedly and by the fifth to seventh day a fully mature schizont is formed, containing from 800 to 1000 merozoites. By the rupture of the schizont the merozoites escape; many of these reach the blood stream, invade the red blood cells, and start the blood cycle. Whether the developmental cycle of the sporozoites may occur in other tissues has not been determined. The sporozoite cycles for *P. falciparum* and *P. malariae* are still unknown.

The blood cycles of the other species of malarial organisms correspond very closely to that of *P. vivax*. The time of sporulation differs—that of *P. malariae* taking place at the end of three days and the rise of temperature occurring on the following day; that of *P. falciparum* taking place irregularly in from 24 to 48 hours so that the rise in temperature of the patient is irregular; that of *P. ovale* is about the same as for *P. vivax*. Of course, people suffering from malaria may have two species present or a double infection of any one, and this complicates the clinical picture of the disease.

In order that the exogenous phase of the malaria parasites may be completed in a susceptible mosquito and the infected mosquito live long enough to transmit the infection, certain climatic conditions appear essential. With *P. vivax* the temperature must be over 62° F. (16.6° C.), optimum 77° F.

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[1] New names, many of them, have been used to designate these stages but no uniformity has been reached.

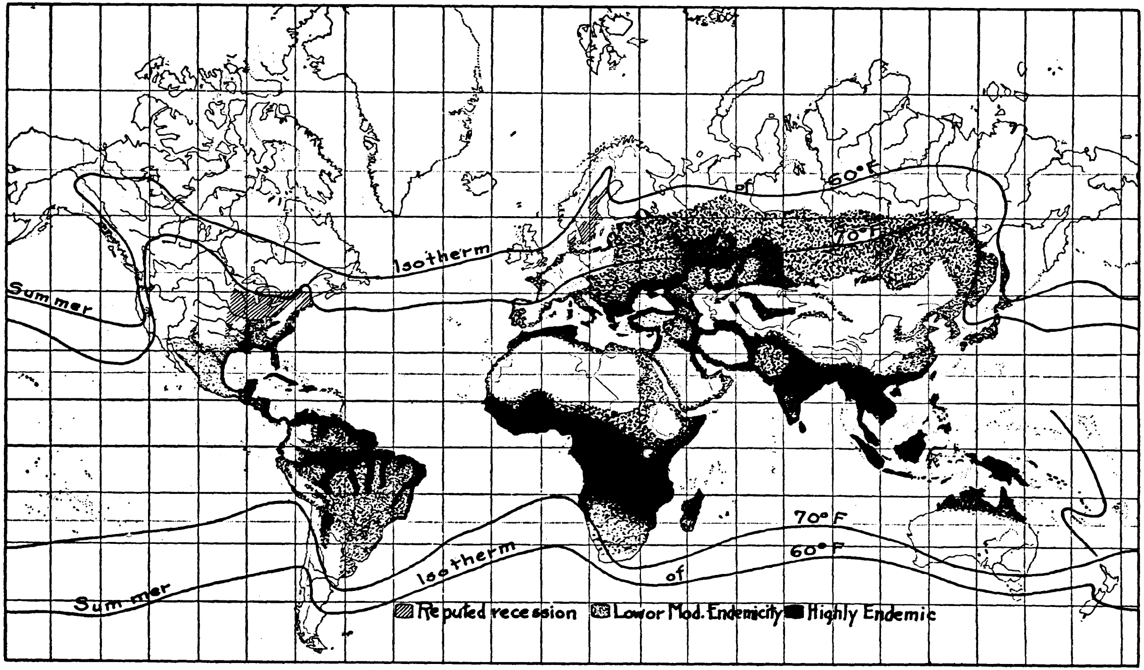

60°F
70°F
Isotherm
Summer
of
70° F
60° F
Isotherm
of
Summer
▨ Reputed recession
▩ Low or Mod. Endemicity
■ Highly Endemic

Fig. 134. General geographical distribution of malaria through the world. The dense black areas show where malaria is highly endemic and epidemic; the dotted areas indicate that malaria is endemic though rarely epidemic; the slanting lines in North America show where malaria has largely disappeared. (Modified from Boyd.)

(25° C.), and the relative humidity over 70 per cent; with *P. falciparum* the temperature must be over 68° F. (20° C.), optimum 86° F. (30° C.) and the relative humidity at least 70 per cent. According to Gill (1938), vivax malaria can only maintain itself in temperate zones where the mean temperature during the hottest months of the year (July or August in the Northern hemisphere and January or February in the Southern hemisphere) lies between 60.8° F. (16° C.) and 68° F. (20° C.) or higher and where the mean monthly relative humidity does not fall below 70 per cent. For the malignant type (*P. falciparum*) the temperature must be about or over 68° F. (20° C.), optimum 86° F. (30° C.), and the relative humidity near 70 per cent. Though these are not absolute values, yet, according to Gill (1938), they largely govern the distribution of malaria though not the distribution of anopheline mosquitoes capable of transmitting malaria. Thus, in general, the global area where malaria may be endemic lies south of the summer isotherm of 60° F. in the Northern hemisphere and north of the 70° F. summer isotherm of the Southern hemisphere (Fig. 134) and in regions where temperature and relative humidity are such as to furnish suitable conditions for the completion of the exogenous cycle of the parasite and permit the mosquito to live long enough to infect new hosts.

SOURCES OF ANOPHELINE INFECTIONS: In order that malaria may occur and maintain itself in any given region, certain conditions are essential. The climatic conditions must largely correspond to those outlined in the preceding paragraph. There must be persons who have in their blood the micro- and macrogametocytes of one or more of the malarial parasites; there must also be present a species of *Anopheles* that feeds on man and can act as a transmitter; and, finally, this anopheline must be present in reasonable numbers to ensure adequate infection. The only known source of the gametocytes is man; no animal, either in the wild or under laboratory conditions, has yet been found in which the human malarial parasites can develop. There are at least three types of human "carriers": (1) persons who have had the disease, recovered, and carry the gametocytes in their blood; (2) persons who have the parasites and gametocytes in their blood but have never suffered clinical symptoms of the disease; and (3) persons who have the disease and continue to suffer relapses from time to time. The first two types are known as "latent" carriers and are a constant menace to the general population in any malarious region. The last type is probably as dangerous because, with the frequent recurrence of the disease, excessive numbers of the gametocytes may develop. Craig and Faust (1940) state that about 33 per cent of those having malignant malaria will carry gametocytes and hence are "carriers" while over 50 per cent of those with vivax malaria will normally be "carriers" with gametocytes in their blood. However, it has been demonstrated again and again that "carriers" with gametocytes in their blood may not infect susceptible mosquitoes while other "carriers" with only a few or nondemonstrable gametocytes may infect anophelines. The reason for this is not easy of explanation.

Given a source of the parasites, the only other requirement for an outbreak of the disease is adequate numbers of a species of *Anopheles* which readily bites man and in which the sexual and sporogenous cycle can be completed. Not all human beings are *good* "carriers"; neither are all anophelines *good* transmitters of malaria. This condition is certainly fortunate, for if all our anophelines were good transmitters the difficulties in the reduction and control of malaria would be greatly enhanced. Unfortunately we do not know all the "good" transmitters or all the "poor" transmitters among the anophelines. Furthermore, it is well known that the same species of *Anopheles* may be a good or "dangerous" transmitter in one region (*A. pseudopunctipennis* in parts of Argentina and Mexico; *A. subpictus* (*rossi*) and *A. hyrcanus* in the Dutch East Indies) and a poor transmitter of the disease in another region (*A. pseudopunctipennis* in California; *A. subpictus* (*rossi*) and *A. hyrcanus* in British India). Table 7 based on all available literature gives the principal "good" or "dangerous" transmitters known from the world and the general region where they are known to transmit malaria.

In Table 7 some species are recorded as "good" or "dangerous" transmitters of malaria either from known surveys or based on epidemiological grounds. About another score could be added, based on experimental infections under laboratory conditions or the finding of a few naturally infected forms in the wild. In North America the principal transmitters are *A. quadrimaculatus* and *A. freeborni*. *A. crucians* is readily infected under laboratory conditions and undoubtedly acts as a transmitter in parts of its range. Though *A. punctipennis,* our most widely distributed species, is susceptible to infection, yet the role it plays in the spread of the disease is considered unimportant. *A. atropos* has recently been shown susceptible to infection and it probably acts as a transmitter within its range; *A. walkeri* has been found infected in the wild and is readily infected under experimental conditions.

NATURAL INFECTION IN ANOPHELINES: Based on an examination of all available literature, nearly sixty different species or varieties of *Anopheles* have been recorded (from dissections) as having either gut or salivary gland infections (natural). In order that malaria can exist in any region there must be present anopheline mosquitoes naturally infected with the parasites. If no such infections occur and if there are no human "carriers," *Table 7*. The principal vectors of malaria throughout the world (52 species).

North America north of Mexico

Species	Range	Larval habitats
A. freeborni Aitken	Southern Oregon, California in drier regions, New Mexico, western Texas	Fresh seepages, irrigation ditches, rice fields, streams, in open sunlight
A. quadrimaculatus Say	Massachusetts west through Ontario to Minnesota south to central Texas, Gulf coast of Mexico, and east to Atlantic coast	Lakes, ponds, lime sinks, impounded waters, fresh marshes, swamps, bayous, grassy pools, among driftwood, etc. Vegetation usually abundant

Mexico and Central America

A. (*N.*) *albimanus* Wied.	Southeastern Texas, through Mexico, Central America, to Colombia, Ecuador, and Venezuela; the West Indies	Pools, puddles, hoof prints, ponds, marshes, swamps, fresh or brackish lagoons, artificial containers, almost any kind of fresh water with exposure to sunlight
A. (*N.*) *aquasalis* Curry	Nicaragua, Panama, Trinidad, Lesser Antilles, northern Brazil to Alagoas	Tidal marshes of rivers, brackish lagoons, irrigation waters (mostly along seacoasts in tidal areas)
A. (*Kerteszia*) *bellator* D. & K. Important vector in Trinidad	Trinidad, Venezuela	Breeds only in water in epiphytic bromeliads (especially "wild pineapples")
A. (*N.*) *darlingi* Root	Mexico (Tabasco), Br. Honduras, Guatemala, Venezuela, south along Andean foothills to Argentina & Chile	Fresh-water marshes, lagoons, seepages, overflows of rivers, streams, etc., with vegetation and exposed to sunlight
A. (*A.*) *pseudopunctipennis pseudopunctipennis* Theo. Vector in parts of range	California to Utah, east to great plains and south through Mexico, Central America, to Argentina and Chile	Clean seepages, pools, impounded water, puddles, streams with algae; more or less open to sunlight

South America

A. (*N.*) *albimanus* Wied.	See above	
A. (*N.*) *albitarsis* Lyn. Arrib. Vector in some parts of range	Guatemala south through Central America to Paraguay; Trinidad	In mats of aquatic vegetation in large ponds, marshes, lagoons, bayous of flooding rivers, and not too much shade

Species	Range	Larval habitats
A. (*N.*) *darlingi* Root	See above	See above
A. (*M.*) *gambiae* Giles	Established in northeast Brazil; now exterminated (?)	See below
A. (*A.*) *pseudopunctipennis pseudopunctipennis* Theo.	See above	See above
A. (*N.*) *pessoai* Galvao & Lane Vector of malaria in the Amazon basin	Colombia south through Brazil	Open shallow pools with grass and algae

Europe, North Africa, and the Near East

(*A.* (*A.*) *maculipennis* complex) 1. *A. labranchiae atroparvus* van Thiel Vector in England, Netherlands, Spain, Portugal, Germany & Siberia	Widely distributed in Europe and Asia from England to Japan; from Sweden and maritime Siberia south to Spain and n.e. Italy; Mongolia	Typically in brackish water along coastal areas but also occurs in fresh water inland as marshes, swamps, lagoons, and any suitable water more or less exposed to sunlight
2. *A. labranchiae labranchiae* Falleroni Vector in its range	S. Spain, Italy, Dalmatian coast, Sicily, Sardinia, Corsica, n.w. coast of Africa	Brackish water in coastal marshes, fresh water in rice fields, upland streams, and in many types of water
3. *A.* (*A.*) *messae* Falleroni Vector in Romania & probably elsewhere	From Norway and Sweden south to Italy & from Britain east to Black Sea and e. Siberia	Cool fresh, standing bodies of water in large inland river valleys, ponds, lakes, and marshes
A. (*A.*) *claviger* Meig. (*bifurcatus*) Vector in Palestine and Syria	Europe, Northern Africa, Turkestan, Asia Minor	Marshes, rock pools, wells, cisterns
A. (*M.*) *multicolor* Cambouliu Vector on epidemiological grounds	North Africa (desert areas), Egypt, Sudan, Cyprus, Anatolia, Palestine, e. Persia, Baluchistan	Pools, stagnant or slow-flowing drains, shallow wells; pools fresh or saline; desert pools of high salinity
A. (*M.*) *pharoensis* Theobald Vector in Nile province, Sudan	Widespread in Africa, Madagascar, Palestine	Swamps and rice fields with vegetation
A. (*A.*) *sacharovi* Favr (*elutus*) Vector in Balkans, Palestine, Near East	N.e. and central Italy, Sardinia, Corsica, Balkans, central Russia, east to west China, Iran, Iraq	Coastal and inland marshes, fresh or brackish; seems to prefer sunlight

Table 7.—Continued.

Species	Range	Larval habitats
A. (*M.*) *sergenti* Theobald Vector in Egypt & Palestine	Canaries, Algeria, Tunisia, Egypt, Syria, Turkey, Palestine, n.w. India	Rice fields, borrow pits, irrigation ditches, drains, seepages
A. (*M.*) *superpictus* Grassi Vector in S. Europe, Mesopotamia, Baluchistan	Spain across southern Europe, Asia Minor, Syria, Palestine, to s.w. India	Pools in hilly stream beds, rivers, irrigation water, seepages, all more or less open to the sun
Africa mainly south of the Sahara Desert		
A. (*M.*) *funestus* Giles Vector throughout its range	Throughout tropical Africa north into Ethiopia and south to Natal; Mauritius	Swamps, weedy margins of streams & rivers, furrows, lakes, ponds, ditches, seepage areas
A. (*M.*) *gambiae* Giles Vector in its range	Tropical Africa, Sudan north to southern Egypt, Arabia, Madagascar, Mauritius, Reunion	Pools, hoofprints, puddles, seepage, water holes, drains, pools in stream beds
var. *melas* Theo.	More or less a coastal form	Both fresh and saline water
A. (*M.*) *hancocki* Edw. Vector in its range, especially when abundant	Sierra Leone, Liberia, Nigeria, Cameroons, Belgian Congo, Uganda	Grassy water holes, grassy ditches, native wells, streams, swamps
A. (*M.*) *hargreavesi* Evans Vector in its range, especially when abundant	Sierra Leone, Liberia, Gold Coast, s. Nigeria, Gaboon, Belgian Congo	Among *Pistia* in open and jungle pools, swamps, stream margins
A. (*M.*) *moucheti* Evans Vector when in numbers	Cameroons, central & eastern Belgian Congo, Uganda	Grassy pools, margins of streams, swamps; vegetation usually present
var. *nigeriensis* Evans Vector when abundant	Southern Nigeria	Clear water with *Pistia,* swamps among vegetation
A. (*M.*) *nili* Theobald Heavily infected in nature	Sierra Leone east to Sudan and south to Mozambique & Zululand	Margins of streams in deep shade with vegetation; also in clean running water with little shade; swamps, ditches
A. (*M.*) *pharoensis*	See above	
A. (*M.*) *pretoriensis* Theobald Not considered important	Gold Coast across Africa to Somaliland south to Transvaal & Natal; Aden	Rock pools, semistagnant pools in streams and ditches, shallow puddles, hoofprints; vegetation usually absent

Oriental Region

(India, Ceylon, Burma, Malaya, China, Dutch East Indies, Philippines, and the other islands in this region)

Species	Range	Larval habitats
A. (*M.*) *aconitus* Doenitz (Feeds mainly on animals) Vector in Indo-China	India, Ceylon, Burma, s. China, Malayan region, Neth. Indies, Borneo, Celebes, Philippines; widely distributed	Rice fields, streams, pools, drains, swamps, irrigation ditches, reservoirs, and similar situations
A. (*M.*) *culicifacies* Giles Important vector in India, Ceylon	Baluchistan to Burma south to Ceylon; also reported from Yünnan, Siam, Tonkin	Pools, pits, wells, rice fields, pools in river beds, rock quarries, irrigation channels, slow-flowing streams; fresh water but tolerates brackish
A. (*M.*) *annularis* v. d. Wulp	India, Ceylon, Burma, s. China, Formosa, Siam, Indo-China, Malayan region, Neth. Indies, Philippines, Borneo	Every type of water, pure or stagnant, contaminated; seepages, spring pools, flowing streams
A. (*M.*) *fluviatilis* James Vector throughout its range	S. China, India, Burma, Siam, Turkestan, Baluchistan. Mostly in foothills in its range	Clean hill streams, pools in ravines, stream beds, irrigation channels, behind boulders in swift water, seepage holes; prefers sunlight
A. (*A.*) *hyrcanus sinensis* Wied. Known vector in China, s. Japan, Indo-China, Ned. Ind.	N. e. India, Burma, China, Indo-China, Korea, Japan, Formosa	Stagnant water of rice fields, pools, swamps, ponds, lakes, slow streams
A. (*M.*) *jeyporiensis candidiensis* Koidzumi Vector in Tonkin	India, China, Burma, Formosa, Indo-China	Flowing water in ditches, seepage water
A. (*M.*) *jeyporiensis jeyporiensis* James Not important vector in India	Eastern India and probably Indo-China	Flowing water in irrigation ditches, marshy edges of streams, lakes, and ponds
A. (*M.*) *leucosphyrus* Doenitz Vector in India, Burma, Borneo, Neth. Indies	India, Ceylon, Burma, Malaya, Sumatra, Java, Borneo, Philippines, Indo-China	Heavily shaded pools in beds of mountain streams, drains, elephant foot prints, wells; jungle breeder
A. (*M.*) *maculatus* Theobald Vector in Malaya, Neth. Indies, & Assam (?)	India, Ceylon, Burma, s. China, Siam, Malaya, Neth. Indies, Formosa, Philippines, Indo-China	Pools in swift streams obstructed by boulders, pools, rice fields, lake margins; prefers sunlight

Table 7.—Continued.

Species	Range	Larval habitats
A. (*M.*) *minimus* Theo. Important vector in its range (Man is the preferred host)	E. & n. India, Ceylon, Burma, Assam, Siam, Indo-China, s. China, Formosa	Foothill streams, springs, irrigation ditches, terraced rice fields, seepages; breeds in sunlight waters
A. (*M.*) *minimus flavirostris* (Ludlow) Vector in the Philippines	Islands of the Philippine group, Celebes, Java	As above for *minimus*
A. (*M.*) *mangyanus* (Banks) Vector on epidemiological evidence	Many islands of the Philippines	Shallow, slow-flowing streams in or close to foothills, irrigation ditches, often in mats of vegetation; prefers sunlight
A. (*M.*) *philippinensis* Ludlow Vector in Bengal; said not to be in the Philippines	India, Burma, Malaya, Siam, Neth. Indies, s. China, Philippines	Tanks, pools, drains, rice fields, swamps, ditches, pits
A. (*M.*) *stephensi stephensi* Liston Important vector in urban areas; important in its range	Eastern Arabia, s. Iraq, Iran, India, Burma	Wells, cisterns, flower pots, artificial receptacles, roof gutters, temporary water
A. (*M.*) *subpictus* Grassi Known vector in Celebes	India, Malaya, Yünnan, Neth. Indies, New Guinea, Indo-China	Borrow pits, buffalo wallows, brick pits, furrows in gardens, roof gutters; contaminated water, even brackish
A. (*M.*) *sundaicus* (Rodenwaldt) Vector throughout its range	India, Burma, Siam, Malaya, Sumatra, Java, Borneo, Lesser Sunda Isls., s. Celebes	Brackish or salt-water lagoons and swamps, pools of brackish water behind coastal embankments, tidal drains, and similar places
A. (*M.*) *superpictus* Grassi	See above	
A. (*M.*) *umbrosus* (Theobald) Vector in some areas of its range	East India, Tonkin, Malaya, Cochin-China, Sumatra, Java, Borneo, Celebes	Shaded stagnant pools & jungle morasses; (brackish water in mangrove swamps, = *A. baezai* Gater)
A. (*A.*) *barbirostris* v.d. Wulp Not considered an important vector	India, Ceylon, Burma, Siam, China, Malaya, Borneo, Sumatra, Java, Lesser Sundas, Celebes, New Guinea, Philippine Isl.	Deep stagnant water with vegetation and preferably in shade as margins of rivers, lakes, swamps, pools from springs, canals, rice fields, saline swamps
A. (*M.*) *kochi* Dönitz Found infected in India & Neth. Indies	India, Burma, Malaya, s. China, Sumatra, Java, Borneo, Lesser Sundas, Philippines, Moluccas	Small muddy pools, unplanted rice fields, streams, irrigation ditches, artificial containers

Australasian Region

(Australia, Tasmania, New Zealand, Islands eastward to 180°, New Guinea and islands north to equator and west to oriental region)

Species	Range	Larval habitats
A. (*M.*) *annulipes* Wlk. Only on epidemiological evidence	Coastal and inland Australia, Tasmania, New Guinea. Breeds at elevations of 5000 ft.	Grassy pools, edges of marshes, slow-running creeks, hoofprints, rock pools; at times in brackish water
A. (*A.*) *bancrofti* Giles Found infected in New Guinea	New Guinea, northern Australia	Shallow water overgrown with vegetation in streams, and similar situations; prefers shade
A. (*M.*) *farauti* Laveran Dominant vector in its range	E. New Guinea, New Britain, Solomons, New Hebrides, n. Australia	River & stream margins with vegetation, springs, wells, hog wallows, ruts, holes, hoofprints, ditches, and artificial receptacles as boats, tanks, drums, etc.
A. (*M.*) *lungae* Belkin & Schlosser Vector in some parts as Guadalcanal (?)	Guadalcanal	In the jungle in seepage areas, potholes in streams, rock holes, dense jungle swamps, & temporary pools
A. (*M.*) *punctulatus* Doenitz Vector in New Guinea	Moluccas, New Guinea, New Ireland, Solomons, & adjacent islands	Rain pools, road ruts, footprints, potholes in drying stream beds; pools may be muddy and free of vegetation; sunlight loving

malaria will be absent despite the abundance of "good" or "dangerous" anopheline transmitters. The introduction of human "carriers" is all that would be necessary for an outbreak of the disease. Boyd (1930) summarizes many of the dissections of anophelines made in order to determine the rate of natural infection. The results show a rather low "rate" of natural infection, though the rate must vary widely since it depends on many factors. In the United States, as summarized by Root, *Anopheles quadrimaculatus* shows a percentage infection of 1.47 (8864 dissections); *A. punctipennis,* 0.18 (543 dissections); and *A. crucians,* 0.25 (1203 dissections). King (1922, 1939) reports an infection rate of 0.107 per cent (sporozoite) in 9340 dissections of *A. quadrimaculatus* at Mound, Louisiana. In South America out of a dissection of 2666 *A. albitarsis* only 25 were found infected (all from Brazil). Causey, Deane, and Deane (1946) report a 10 per cent infection in *A. gambiae* found in houses and 5.6 per cent in those taken in the wild, but Davis (1931) reports 62.8 per cent natural infections in 172 mosquitoes collected in houses at Natal, Brazil. In dissections of 7486 *A. albimanus* 53 were reported infected. *A. darlingi* has a high rate of infection from a maximum of 88.8 per cent in British Guiana

(222 infected out of 250 dissected; Kenney, 1946) to as low as 1.8 per cent (1513 dissected; Deane, Causey and Deane, 1946). *A. pseudopunctipennis* showed 12 infected out of 435 dissected in Argentina (Davis, 1927), but Patterson (1911) reported 1.03 per cent infection in 1549 dissections. Vargas *et al.* (1941) record 12 gut infections out of 526 dissections and 4 gland infections in 1246 dissections in Mexico. Downs *et al.* found 46 oocyst infections (3.3 per cent) in 1383 *A. aquasalis* dissected (collected in houses in Trinidad) but out of 1364 only 1 with gland infection; in *A. bellator* they record 10 stomach infections (0.78 percent) in 1263 dissections. In Africa *A. funestus* varies in its infection rate from 3 per cent (20,000 dissected in Kenya; Garnham, 1938) to 12.5 per cent at Freetown (Gordon, 1932). *A. gambiae* is reported by Gordon *et al.* (1932) to have an infection rate of over 11 per cent at Freetown. Barber and Olinger (1931) found 1798 infected out of 14,904 dissections (12.6 per cent made in Southern Nigeria. (The sporozoite rate varied from 2.2 to 30.5 per cent, according to the place where the mosquitoes were taken.) In Europe the main vector is *A. maculipennis* or its varieties. Dissections of this species show a low infection rate: in Macedonia 0.73 per cent in 14,713 dissections (Rice and Barber, 1935) and in Greek Macedonia 0.08 per cent (15,461 dissections) and a rate of 0.30 per cent in 1311 dissections of mosquitoes taken from one house on one day (Barber and Rice, 1937). Swellengrebel and de Buck (1938) report 5.58 per cent infected out of 44,167 dissections of *A. maculipennis atroparvus* (short wings) taken in houses in Holland but only 1 infected of *A. maculipennis messae* (long wings) out of 2880 dissected.

DURATION OF INFECTION IN THE MOSQUITO: How long the malarial parasites can survive in the salivary glands of mosquitoes has been partially determined in a number of instances. The ability of the sporozoites to survive for long periods and infect new hosts when the mosquito bites is of great importance. Mayne (1922), using *Anopheles punctipennis* infected with *Plasmodium falciparum,* recovered the sporozoites (by staining) in the salivary glands for 68, 70, 71, 83, and 92 days after infection. He produced infection in a human host by the bite of a mosquito that had been infected 55 days previously. This same mosquito failed to infect on the 67th day but dissection on the 68th day showed living sporozoites. Boyd *et al.* (1936) report that *A. quadrimaculatus* infected experimentally with *P. falciparum* could transmit the disease for at least 40 days after the extrinsic developmental cycle; they proved valueless after 50 days.

James and Shute (1926) kept batches of *A. maculipennis* infected with *P. vivax* at temperatures of 4° C. (37.4° F.) to 6° C. (42.8° F.) and these retained their infectivity for two and one-half months. James (1927) reports a group of

A. maculipennis that retained infectivity for nearly six months; some of these were later reinfected and proved capable of transmitting malaria. Some of the reinfected specimens lived as long as three months after the reinfection. It has generally been assumed that malaria parasites cannot survive in the anopheline mosquitoes during hibernation, especially in the colder climates. King (1917) showed that *P. vivax* could survive in *A. quadrimaculatus* at a temperature of 30° F. (—1° C.) for at least two days; at 31° F. for four days; and at a mean temperature of 46° F. (7.8° C.) for seventeen days. He also found that *P. falciparum* could resist temperatures as low as 35° F. (1.7° C.) for at least one day.

James (1927) concludes from his observations on specimens of *A. maculipennis* that were infected with *P. vivax* and that remained infective for six weeks in spite of refrigeration at 3° to 6° C. that the tertian malaria organism might survive the winter in hibernating anophelines and thus produce primary attacks of malaria in winter and early spring. Inasmuch as many anopheline species in the north habitually seek out human habitations for the purpose of hibernation, there would seem to be no question that such individuals, if infected late in the autumn (natural infections are recorded from dissections as late as October 20 and November 1, at Lenwil, Louisiana; October 4, at Mound, Louisiana; and October 25, at Edenton, North Carolina) could remain capable of infecting human hosts during the winter and early spring. Swellengrebel and de Buck (1938) demonstrated that naturally infected *A. maculipennis atroparvus* in Holland lose their ability to transmit vivax malaria after December, for at that time the sporozoites are dead and there is no transmission during winter and early spring, though this mosquito feeds on man during winter and spring. However, the temperature is below that required for the extrinsic cycle of the parasite. All the spring malaria consists of relapses (primary) from infection received the preceding autumn. New infections occur only late in July to October when the temperature and relative humidity are right for the extrinsic development of the parasite.

CONTROL OF MALARIA: The problem of malaria control consists in the breaking of the etiological chain at some vulnerable point. This could be done by any one of the following methods if we only knew some effective procedure:

1. Elimination of the human "carriers." No very useful therapeutic measures are at present known by which the gametocytes can be destroyed in the circulating blood. Atebrine and quinine give indications of value; the new drugs paludrine, aralen, and pentaquine give some hope of success; and other drugs may yet be found, but it seems doubtful if such a beneficent drug

can be discovered. This part of the etiological chain, then, remains unbroken.

2. The successful treatment of malarial patients so as to effect a cure and prevent the formation of gametocytes. Quinine and its derivatives have been the standard treatments, but they do not completely cure or prevent the formation of gametocytes. Atebrine, aralen, pentaquine, and paludrine are drugs of great value, but they are not perfect cures. Furthermore, if a successful treatment were known, this would not eliminate the first type of "latent" malarial carriers, though it would undoubtedly in time.

3. Elimination of the anopheline transmitters. This is possible when we know more about anopheline biology and methods of control that are financially practicable. This procedure would seem, at present at least, the most feasible and, from experimental work so far carried out, the most efficient. For methods of control of mosquitoes see Chapter XII.

Several palliative measures can be employed. These consist of effective screening of malarial patients against anophelines and the use of screens and bednets by the general population in malarious regions. These measures, when adequately carried out, will greatly reduce the incidence of malaria. At the present time a combination of all these measures, however ineffective any one of them may be, is our best procedure in reducing the malarial scourge.

BLACKWATER FEVER

Blackwater fever is a severe fever of unknown etiology accompanied by prostrating chills, profuse vomiting, great destruction of the red cells (hemolysis), and the passage of hemoglobin in the urine (the urine is a mahogany color, hence the name of the disease). At present it is apparently quite generally accepted that blackwater fever is probably due to repeated attack or continuous infection with malaria. Apparently many cases develop during the treatment of malaria with quinine, and the administration of quinine may play some part in the genesis of the attack. The disease is widely distributed throughout the tropical and subtropical regions of the world and is most prevalent in the intensely malarious sections. In the Americas it occurs in the northern area of South America, the Central Americas, the West Indies, and parts of the southern states of the United States. Recently Stephens made an extended study of the incidence of this disease throughout the world and he shows that in the United States it has occurred in at least 18 states and as far north as New York, Illinois, Colorado, and California. Blackwater fever is a very severe disease with a high mortality. Apparently it can only be prevented by the avoidance of long and continued attacks of malaria. It has many complications and a person who has recovered from an attack should not continue to live in a highly malarious region. In order to reduce the incidence of the disease in any area the most logical procedure, based on our present knowledge of the disease, would be the destruction of malaria-carrying anophelines.

YELLOW FEVER

Yellow fever is one of the most virulent of human diseases. Until recently it was believed that the disease was of American origin and its transmitter, *Aedes aegypti,* an American species of mosquito. Accumulating evidence has definitely established the original home both of the disease and the mosquito to have been Central West Africa, whence they have been carried to the Americas. Though the mosquito has been carried by commerce to practically all regions of the globe where it can maintain itself, it does appear rather curious that the Americas became a permanent home of yellow fever. Carter in 1922 gave the Caribbean littoral as the probable original home of the disease, but the same author in 1930 reached the conclusion, based both on historical and biological (very strong evidence) grounds, that Africa was the original home.

DISTRIBUTION: At present yellow fever is widely distributed. It is known to be endemic in Brazil, the Amazon basin, Colombia, Venezuela, Peru, Bolivia, and probably other South American areas, and in Africa it extends from the west coast south of the Sahara into the Anglo-Egyptian Sudan, Uganda, Tanganyika, Ethiopia (?), and the great valley of the Niger.

Formerly yellow fever was rather widespread around the Caribbean Sea and was introduced from time to time to northern cities, where numerous epidemics occurred during the summer. This disease, so highly fatal to non-immunes, remained a mystery till Reed, Carroll, Lazear, and Agramonte finally established, in 1900, that it could be transmitted from the sick to the well only by a mosquito, the tiger mosquito (*Aedes fasciatus, Aedes argenteus, Stegomyia fasciata,* or *Aedes aegypti;* unfortunately this mosquito has a long list of synonyms). Their conclusions have been well established and the etiological chain in this disease is again the parasite (a virus), the man with the parasite (the patient), the mosquito, and finally a new patient. Noguchi isolated an organism, *Leptospira icteroides,* which he claimed was the etiological agent, but recent work has clearly shown that it is not—that it is only *Leptospira icterohaemorrhagiae* (= *interrogans*), the causative agent of infectious jaundice (Weil's disease). The causative agent is a virus.

Yellow fever is an acute, febrile, noncontagious disease, characterized by profound prostration, jaundice, hemorrhages, and albuminuria. The death rate is very high. A single attack confers immunity. The incubation period in man is generally three to seven days, though it may be shorter (two days) or somewhat prolonged (very rarely). However, the causative agent is normally present in the blood stream of man only during the first three or four days after the onset of the disease. Whether it is present before the initial attack is still undetermined, though work with monkeys would indicate that it probably is. The period during which the parasite is present in the blood stream is of great significance when the infection of the mosquito carrier is considered. The importance of the mosquito in the spread of the disease may be stated very briefly. In order to obtain the parasite the mosquito (*Aedes aegypti*) must bite a patient during the first three or rarely four days after the initial attack. Within the mosquito the parasite undergoes a developmental cycle, for it is not till 9 (at temperatures of 28° C.) to 14 days later that the mosquito is capable of infecting a susceptible person. Once infected the mosquito remains capable of transmitting the disease to nonimmunes as long as it lives. How long an infected mosquito can live in nature is not easy to determine, but under experimental conditions infection has been transferred 59 days (one case), and 118 days (Hindle, 1931) after the infecting meal. Bauer (1940) reports keeping an infected *A. aegypti* alive for 200 days. A single bite of an infected mosquito may bring about an attack of the disease.

Until the year 1928 it was generally accepted that the yellow-fever chain consisted of the human patient (no other animals were known to be susceptible), the yellow-fever mosquito (*Aedes aegypti*), and susceptible or nonimmune human individuals. As there is no known specific treatment for the disease, all efforts were concentrated on the reduction or elimination of the mosquito in attempts to control yellow fever. So successful has this procedure been that practically the entire yellow-fever areas in the Americas have been rendered free from the disease. However, sporadic outbreaks, and these widely separated, have occurred and still occur in certain sections of South America. The endemic center in West Africa presented a problem and a serious menace as a possible focus for the continued spread of the disease. The investigations carried on at Lagos and at other African points have resulted in the reexamination of the entire yellow-fever problem. Stokes, Bauer, and Hudson (1928) for the first time demonstrated that monkeys (*Macacus rhesus*) were susceptible to the disease, producing fatal infections in two monkeys by the bites of *Aedes aegypti* 85 and 91 days after the mosquito obtained its infective blood meal. Since then a long list of different species of monkeys has been shown to be susceptible. In 1928 Bauer showed that other species of mosquitoes, *Aedes stokesi* Evans (*apicoannulatus* Edw.), *Aedes luteocephalus* Newst., and *Eretmapodites chrysogaster* Graham, could act as transmitters of yellow fever. The results of Bauer's work have been fully confirmed and numerous investigations have since added other species of mosquitoes from various parts of the world.

Yellow fever demonstrated its versatility when in 1933 Soper reported a jungle outbreak far from the presence of *Aedes aegypti* or any other known vector of the disease. Known now as "jungle yellow fever," it shows the same characteristics as the classical type (urban) but its source and all its vectors have yet to be determined. Those known at present are listed below and the suspected animal reservoirs are indicated. The existence of jungle yellow fever will always be a menace, for an infected person or persons may visit the more distant urban centers (as by airplane) and form a focus for the infection of *Aedes aegypti* (provided it is present in numbers). Jungle yellow fever is widespread in Africa. Recently Smithburn and Haddow (1946) reported the presence of yellow fever in mosquitoes taken from an uninhabited forest in Bwamba (Africa), indicating a cycle of yellow fever without the human factor. The development of a yellow-fever vaccine has been of inestimable value, for millions of people in yellow-fever areas can be readily vaccinated and immunity is of considerable permanence.

These recent results show that the yellow-fever etiological chain is much more complicated than at first thought. There is an animal reservoir other than man and its extent is still unknown. Probably not all the mosquitoes capable of transmitting the disease have yet been discovered. In man it is generally stated that the virus occurs in the blood stream only during the first three or four days after the initial attack. In susceptible monkeys it has been shown that the virus is present in the blood stream from the initial infection till their death and also in their tissues after death. By analogy it might be assumed that man has the virus in his blood shortly after the initial infection, that is, several days before the febrile attack. If true, the period during which mosquitoes can obtain the virus is increased. Again the old question as to whether there are "carriers" has been raised but it has not been finally answered.

The following list presents data on the known mosquitoes that have been found capable of transmitting the disease from monkey to monkey or other experimental animals either by their bites or by a suspension of the ground-up bodies or that have been found infected in the wild:

Table 8. Mosquitoes capable of transmitting yellow fever (excluding *A. aegypti*).

*By bites, naturally.
§Efficient transmitters.
†Experimental transmission by bites.
||Experimental transmission by crushed bodies.
‡Found infected in the wild.

Africa (Ethiopian Region)

Species	General distribution	Larval habitat
†*Aedes aegypti queenslandensis* (Theo.)	Eastern Ethiopian, northern Australia	Domestic, largely artificial containers
*‡§*Aedes africanus* (Theo.)	Widespread	Tree holes, banana stumps; occasionally in artificial containers. Adults tree-canopy-loving, crepuscular
†*Aedes albopictus* (Skuse)	Eastern Ethiopian, Oriental, northern Australia	Tree holes, rock holes, containers; domestic
||*Aedes irritans* (Theo.)	Widely distributed	Crab holes, brackish surface pools
**Aedes luteocephalus* (Newst.)	Widely distributed	Tree holes, bamboo stumps
†*Aedes metallicus* (Edw.)	Widely distributed	Tree holes, coconut shells
||*Aedes nigricephalus* (Theo.)	West African region	Crab holes
||*Aedes punctocostalis* (Theo.)	West African region	Not known. Probably ground forest pools (Hopkins, 1936)
*†‡*Aedes simpsoni* (Theo.)	Widely distributed	Leaf axils of banana, etc., pineapple tops, tree holes, coconut shells. *Adults diurnal*
*†*Aedes stokesi* Evans	West Africa, Uganda	Tree holes, banana and bamboo stumps
†*Aedes taylori* Edw.	Nigeria, East Africa	Tree holes
†*Aedes vittatus* (Bigot)	Widespread; also in Oriental and Australian regions and about Mediterranean	Rock pools, drains, gutters, wells, artificial containers
†*Culex fatigans* Wied.	Widespread in tropics and subtropics	Breeds in all sorts of pools. Domestic.
||*Culex thalassius* Theo.	Widespread	Water holes, crab holes, earth drains, old pots
*†‡*Eretmapodites chrysogaster* Graham	Widely distributed	Tree holes, fallen leaves, banana stumps, artificial containers

Species	General distribution	Larval habitat
*†*Mansonia africanus* (Theo.)	Widely distributed and common in tropical Africa	Larvae attached to aquatic plants
†*Mansonia uniformis* (Theo.)	Ethiopia, Orient, north Australia, n. & s. China, Formosa, Japan	Larvae attached to aquatic plants

Neotropical and Nearctic Regions

South America, Central America, West Indies, U.S.A.

*§*Aedes fluviatilis* (Lutz)	Brazil, Guianas	Rock pools along rivers, ant rings, clay rings
‖*Aedes fulvithorax* (Lutz)	Trinidad, Surinam, Venezuela, Brazil	Tree holes
*†‡*Aedes leucocelaenus* D. & S.	Widely distributed	Tree holes
‖*Aedes nubilus* (Theo.)	West Indies, Central and S. America	Temporary ground pools
‖*Aedes scapularis* (Rond.)	Widespread	Temporary rain pools
‖*Aedes serratus* (Theo.)	Widespread	Temporary rain pools
‖*Aedes taeniorhynchus* (Wied.)	Coastal areas, N., S., & Central America, Mexico; also inland marshes	Brackish pools or at times fresh-water pools
‖*Aedes terrens* Walk.	Mexico, Central America, to Argentina	Tree-hole breeder
†*Aedes triseriatus* Say	North America	Tree holes
*†‡*Haemagogus capricornii* (Lutz)	Panama to Argentina	Tree holes, bamboo stumps
†‡*Haemagogus equinus* Theo.	Mexico to Argentina	Tree holes
*†‡*Haemagogus spegazzinii* var. *falco* Kum *et al.* (syn. *janthinomys*)	Colombia	Tree holes, etc.
†‡*Haemagogus splendens* Will.	Colombia, Guianas, Brazil	Tree holes
‖*Mansonia albicosta* Pery.	Brazil	Attached to aquatic plants

Table 8.—Continued.

Species	General distribution	Larval habitat
||*Mansonia chrysonotum* (Pery.)	Brazil	Attached to aquatic plants
||*Mansonia fasciolata* Lyn. Arrib.	Mexico to Argentina	Attached to aquatic plants
||*Mansonia justamansonia* (Chagas)	Brazil, Colombia	Attached to aquatic plants
||*Mansonia titillans* Walk.	Neotropical	Attached to floating water plants
||*Psorophora cingulata* Fabr.	Central America to Brazil	Temporary rain pools
||*Psorophora ferox* Hum.	Southern Canada to Argentina	Temporary rain pools
||Sabethines (pooled group) *Sabethoides* *Limatus* ‡*Wyeomyia* *Goeldia* *Trichoprosopon*	South American	Forest breeders
†*Aedes geniculatus* (Oliv.)	Europe, Asia Minor	Tree holes

At present the number of known mosquitoes in which the parasite undergoes a cyclical development and can be transferred to susceptible animals is 17 for Africa, 21 for South America, 1 for the Far East and 1 (*Aedes aegypti*) of general distribution, a total of 40 species. In addition other species have been somewhat incriminated by the inoculation of the infected macerated bodies into monkeys. Though this list is large, the importance of many of the species as transmitters of yellow fever to man is probably not great. Their chief significance lies in the fact that all of them are potential transmitters to monkeys or other susceptible animals that may become reservoirs of the virus.

In addition to the above list of mosquitoes the following arthropods are capable of transmitting yellow fever, mechanically, through interrupted feedings: *Stomoxys calcitrans, Ctenocephalides canis, Cimex lectularius* and *C. hemipterus* (feces of these two also infective), *Triatoma megista, Ornithodoros moubata, O. rostrata, Amblyomma cajennense,* and other blood-feeding insects that attack man.

ANIMAL RESERVOIRS: Man, suffering from yellow fever, was long assumed to be the only source for mosquito infection and the consequent spread of the disease. Since the discovery of Stokes and his co-workers (1928) that monkeys are susceptible to yellow fever, a rather long list of the monkeys of the Old and New World have been found susceptible. What this animal reservoir may mean in the future spread of the disease can only be conjectured. It clearly points to a serious condition should the disease reach India and the Far East.

In the Old World many monkeys have been found susceptible: *Macacus rhesus, M. cynomologus, M. sinicus, M. innus, M. nemestrinus, Cercopithecus tantalus, C. nicitans inpangae, Cercocebus torquatus, Erthrocebus patas,* and many others; New World: *Alonatta seniculus, Pithecia monacha, Cebus variegatus, C. versutus, C. flavus, Callithrix albicollis, C. penicillata* (found infected in the wild), *Leontocebus ursulus, Cebus macrocephala, Lagothrix lagotricha, Ateleus ater, Saimiri scireus, Pseudocebus azarae,* and others.

POSSIBLE SPREAD OF YELLOW FEVER: At present the transmitter par excellence, *Aedes aegypti,* continues to breed almost unmolested in its range within the United States and probably also in many parts of Central and South America and the rest of the world. That yellow fever may spread again into regions where it has apparently been eliminated is not only a possibility but a probability. With the development of airplane transportation, the most distant parts of the Americas are brought close to our doors. The introduction of a single incipient case or "carrier" (?) of yellow fever might be sufficient to start a small focus from which the disease could spread with great rapidity. Because of these possibilities, the elimination or reduction of *Aedes aegypti* should be attempted in all places where it now occurs.

In 1932 the Rockefeller Foundation for Medical Research developed a vaccine (a living, modified virus) that has proved of immense value in reducing outbreaks of yellow fever and bringing outbreaks under control. Since that year millions of people in yellow-fever areas and those going to such areas have been vaccinated. A single vaccination confers a longstanding immunity.

DENGUE

Dengue is a noncontagious infectious disease of low mortality. It is frequently known as "breakbone fever." Its onset is characterized by headache, aching eyes, and severe body and limb pains. The causative agent is unknown, but it is a filter-passing organism and is transmitted by mosquitoes. The disease is widespread throughout many tropical and subtropical regions of the world.

It frequently occurs in epidemic or pandemic waves when the great majority of the population may suffer. Chandler and Rice (1923) state that the 1922 epidemic in the United States was preceded by an excessive abundance of mosquitoes, especially *Aedes aegypti.* In Galveston and Houston there were over 60,000 cases, and some 500,000 to 600,000 cases were indicated from Texas alone. In Northern localities the disease appears in the summer or autumn when the mosquito host is prevalent, but it always dies out when cold weather intervenes, killing off the mosquito. In North America dengue is confined largely south of 38° North latitude.

Investigations of Siler and his co-workers (1926) and Simmons and his associates (1930 and 1931) prove that at least two species of mosquitoes, *Aedes aegypti* Linn. and *Aedes albopictus* Skuse, are effective transmitters. Cleland, Bradley, and MacDonald (1906) had already proved that *Aedes aegypti* was an effective transmitter of dengue in Australia. The yellow-fever mosquito was undoubtedly first incriminated by Bancroft (1906). *Culex fatigans* (*quinquefasciatus*), long considered an important transmitter, is now known not to play any significant part in its spread. Simmons (1931) confirmed the findings of Ashburn and Craig (1907) that by interrupted feedings *Culex fatigans* can, mechanically, transmit the disease and in epidemics may play a part in its spread. Furthermore, in Formosa, *Armigeres obturbans* has been shown capable of transmitting the disease under experimental conditions. Recently *Aedes scutellaris* Walk. has been shown to be an important vector in New Guinea and New Hebrides.

The virus of the disease appears to be present in the blood stream from the day before and during the first three or four days of the febrile attack. In order to become infected, the mosquito must bite a dengue patient during these first three to five days. It requires at least eleven (eight according to some workers) days before the mosquito is capable of transmitting the virus to a susceptible person. Once infected the mosquito remains infected throughout its life (70 days experimentally for *Aedes aegypti* and 54 days for *Aedes albopictus*).

As in yellow fever, no experimental animals were formerly known to be susceptible to the disease. Recently Simmons and his associates (1931) have demonstrated that monkeys, *Macacus fuscatus* and *M. philippinensis,* are susceptible, though they show no clinical symptoms. They proved the infection by transfers back by mosquitoes to human volunteers and other monkeys. They found that monkeys from nonendemic centers were more susceptible than those from regions where the disease is prevalent. It would thus appear that monkeys may be of considerable importance in the epidemiology of the disease.

As many people suffering from this disease may have it in mild form, they remain at their daily tasks and are excellent subjects from which large numbers of mosquitoes become infected. The yellow-fever mosquito is the most domesticated of all our species and it is present in large numbers in houses. It bites at all times during the day and even at night. It will thus be seen that a small outbreak may soon become epidemic and spread with great rapidity. The most efficient method of controlling the disease is by the elimination of the mosquito carriers. *Aedes aegypti* occurs throughout the tropical and subtropical regions, while *Aedes albopictus,* having about the same habits, is restricted at present to the Oriental region. It has been recently established in Hawaii.

FILARIASIS

Filariasis is due to an infection with *Wuchereria* (*Filaria*) *bancrofti* Cobbold or *W. malayi* (Brug), roundworms found in the adult stage in man. Filariasis is indigenous throughout a large part of the world and may be said to occur from about 41° North to about 30° South latitude in the Eastern hemisphere and from about 30° North to nearly 30° South latitude in the Western hemisphere. In the United States filariasis occurs only in a small area about Charleston, South Carolina, though at present it is practically extinct.

WUCHERERIA BANCROFTI: The adult worms live together, often coiled up in tangles, in various parts of the lymphatic system. The females discharge their embryos in the lymph channels, whence they gain access to the blood stream. The embryos are generally known as *microfilariae* as they appear in the blood. Manson (1878) discovered that there was a marked periodicity in the appearance of the microfilariae in the peripheral blood, the maximum nocturnal abundance occurring between 10 P.M. and 2 A.M., while during the day they concentrated in the pulmonary vessels, capillaries of the heart, and parts of the kidney. This periodicity led Manson to make his remarkable experiment with the house mosquito (*Culex fatigans*) and to discover the developmental cycle in the intermediate host, the first instance of an insect serving as an intermediate host of any parasite.

Since the work of Manson, extensive studies in the Pacific area have shown there is also a nonperiodic strain of this filaria, the microfilariae being present in the blood stream of infected persons at all times during the day as well as at night. This condition occurs in the Philippines, Fiji, Samoa (where first discovered), Tahiti, and other islands in this region. However the filariae are identical with the periodic form known from the rest of the world.

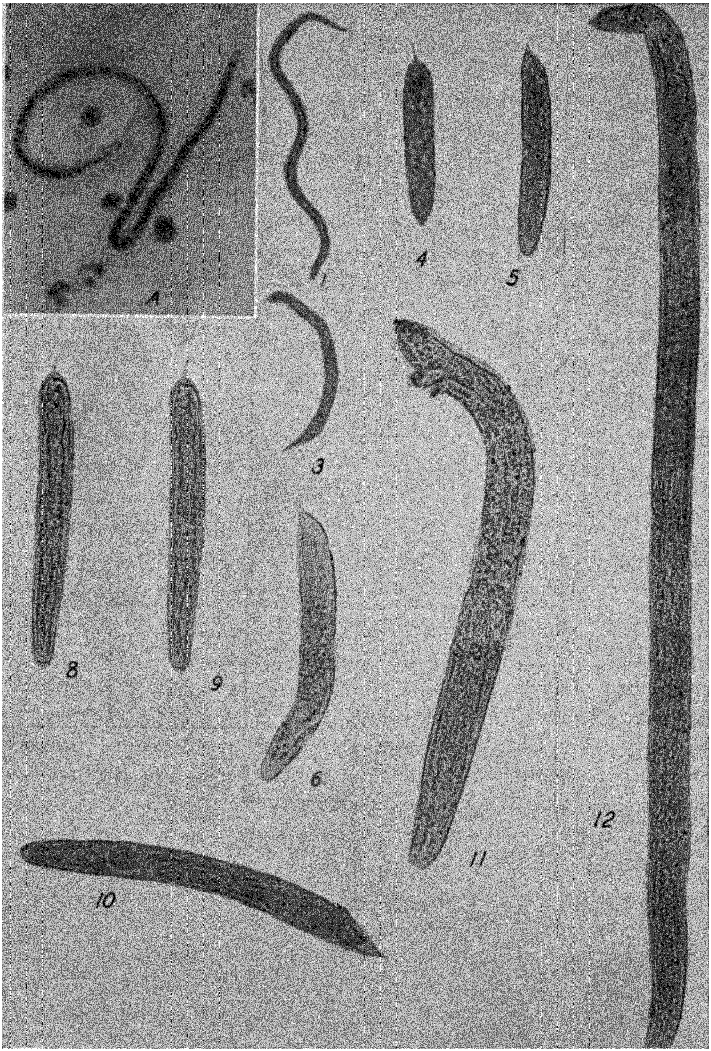
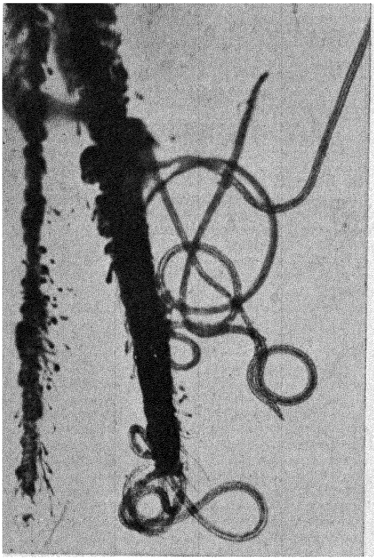


Fig. 135. (*A*) Microfilaria of *Wuchereria bancrofti* in human blood. Nos. 1, 3–6, 8–12 illustrate the development of *Wuchereria bancrofti* by days in the mosquito. The last 4 days (13–16) are not shown because the worm becomes very large. (All photographs from living specimens by R. J. Schlooser; all at the same magnification.)

LIFE CYCLE IN THE MOSQUITO: When blood containing microfilariae (Fig. 135 *A*) is obtained by a susceptible mosquito, the embryos escape from their sheaths and bore through the intestinal wall. In about 24 hours they have all migrated to the thoracic muscles. Here each worm undergoes further development (molting twice), but there is no increase in numbers. In from 11 to 20 days the larval development is complete and the parasites migrate forward to the proboscis. Finally they come to lie, generally in pairs, in the hemocele of the labium. They are now ready to pass to a new host. At the time of taking blood, the worms escape from the labium (Fig. 136) and are said to bore directly through the skin. In due time these larvae reach the lymphatics where they become sexually mature; eventually new generations of microfilariae reach the blood stream. The mosquito is an essential link in the chain in the development and transfer of this parasite.



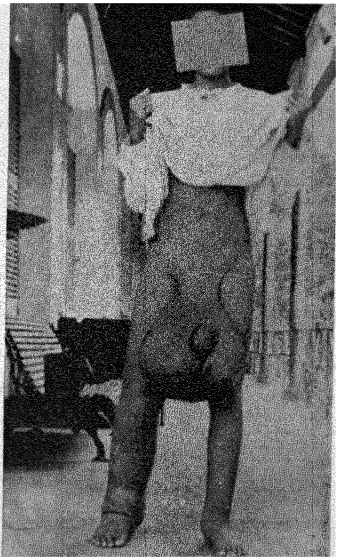


Fig. 136 *(left).* Infective stage of ***Wuchereria bancrofti*** emerging from the proboscis of a mosquito. (Photograph by R. J. Schlooser.)

Fig. 137 *(right).* Elephantiasis. Photograph of a case in Manilla.

The presence of mature filarial worms in man does not necessarily mean a diseased condition. It is frequently associated with marked changes in the lymphatic system, however, and is believed to be responsible for a great variety of organic disturbances, as lymphangitis, adenitis, elephantiasis (Fig. 137), and other complications.

Since Manson's experiments a large number of mosquitoes have been discovered to act as intermediate hosts in the developmental cycle of this roundworm. Most of these discoveries have been made within recent years. The following list, though probably not complete, will give some idea of their numbers and distribution:

Species	*General distribution* (as vectors)
Culex annulirostris Skuse	Dutch East Indies, Celebes
Culex fatigans Wied.	Widespread in tropical and subtropical regions. Good vector
Culex fuscanus Wied.	China (Shanghai area)
Culex pipiens Linn.	Widespread in temperate regions. (Vector in China, Japan, Egypt; readily infected in U.S.A.)
Culex pipiens pallens Coq.	Central China, Japan
Culex tarsalis Coq.	Exp. in the United States
Culex whitmorei Giles	East Indies and Pacific Islands
Culex habilitator D. & K.	West Indies
Culex sinensis Theo.	Poor host in Australia
Culex tritaeniorhynchus Giles	Japan
Culex salinarius Coq.	Exp. in the United States
Culex erraticus D. & K.	Exp. in the United States
Culex pallidothorax Theo.	China, India, Ceylon, Siam, Indo-China
Culex vishnui Theo.	India
Aedes aegypti Linn.	A good vector in some areas (West Africa, Dutch Guiana); not in others; not in the Pacific area
Aedes pseudoscutellaris Theo.	Polynesia (Samoa area)
Aedes scutellaris Walk.	New Guinea, New Hebrides, etc.
Aedes taeniorhynchus Wied.	West Indies (N., S., and C. America)
Aedes thibaulti D. & K.	Exp. in U.S.A.
Aedes togoi Theo.	Japan
Anopheles aconitus Dönitz	Dutch East Indies

Species	*General distribution* (as vectors)
Anopheles albimanus Wied.	Caribbean area
Anopheles albitarsis Lyn. Arrib.	Brazil
Anopheles algeriensis Theo.	Tunis (Africa)
Anopheles amictus Edw.	N. Queensland
Anopheles aquasalis Curry	Brazil
Anopheles bancrofti Giles	New Guinea (?)
Anopheles barbirostris v.d.W.	India, Celebes
Anopheles coustani Lav.	Mauritius
Anopheles crucians Wied.	America (poor vector)
Anopheles darlingi Root	British Guiana
Anopheles farauti Lav.	Solomon Isls., New Hebrides
Anopheles fuliginosus Giles	India
Anopheles funestus Giles	Africa
Anopheles gambiae Giles	Africa
Anopheles hyrcanus nigerrimus Giles	India
Anopheles hyrcanus sinensis Wied.	China, Siam
Anopheles jeyporiensis James	Hong Kong
Anopheles maculatus Theo.	Hong Kong
Anopheles maculipalpus Giles	Mauritius
Anopheles minimus Theo.	Hong Kong
Anopheles pallidus Theo.	India
Anopheles philippinensis Lud.	India
Anopheles ramsayi Covell (*pseudojamesi*)	India
Anopheles punctulatus Dönitz	Solomon Isls., New Guinea
Anopheles rhodesiensis Theo.	Africa
Anopheles splendidus Koid.	Hong Kong
Anopheles squamosus Theo.	Sierra Leone
Anopheles stephensi Listow.	India
Anopheles subpictus Grassi (= *rossi* Giles)	India
Anopheles sundaicus Roden.	India

Species	*General distribution* (as vectors)
Anopheles varuna Iyen.	India
Psorophora confinnis Lyn. Arrib.	Exp. in U.S.A.
Psorophora discolor Coq.	Exp. in U.S.A.
Mansonia africanus Theo.	Africa
Mansonia indianus Edw.	Tonkin
Mansonia juxtamansonius Chagas	Brazil
Mansonia pseudotitillans Theo.	Malaya
Mansonia uniformis Theo.	Africa

The above list (60 species) is rather long but it is not complete. In addition, some 45 species have been found refractory or not easily infected. Furthermore, many of the attempted infection experiments may have failed owing to the conditions under which they were performed. Basu and Rao (1939) demonstrated practically 100 per cent infection of *Culex fatigans* at temperatures of 80° F. and relative humidity of 90 to 100 per cent; at temperatures of 60° F. or below and low humidity infection rarely occurred, or if it did the developmental period in the mosquito was greatly prolonged.

No known drug has much effect on this parasitic worm. Various operative measures are advocated but without great success. The only effective method is the control of the mosquito transmitters in the various regions where filariasis is prevalent. Individuals in endemic areas should exercise great care to protect themselves from the bites of mosquitoes. Along with this should be considered the human carriers in order to reduce mosquito infection.

Recently Brug (1927) described a new species of filaria, *Wuchereria malayi,* from Sumatra. He has shown that nearly 50 per cent of the people are infected with this filarial worm and that it is transmitted by mosquitoes, *Mansonia annulipes* and *M. annulata.* He obtained 83 and 93 per cent infection in the mosquitoes in his experiments, while in nature he found 1 to 2 per cent infection. Other known mosquito vectors include *Mansonia annulifera, M. indianus, M. longipalpis* (= *annulipes*), *M. uniformis, Anopheles barbirostris,* and *A. hyrcanus* var. *sinensis.* At present this filaria is also known from other parts of the East Indies, New Guinea, Celebes, India, Indo-China, parts of China, and nearby regions. In Sumatra infection by this filarial worm results in a high percentage of elephantiasis. The life cycle of this worm in the mosquito is practically identical with that of *W. bancrofti.*

Filariasis is not uncommon in many animals. Dogs suffer from a peculiar filariasis due to *Dirofilaria immitis.* The adult worms are extremely long and slender and are found in the right heart or occasionally in the lungs. A number of mosquitoes serve as the intermediate host. The microfilariae do not undergo their development in the thoracic muscles but in the Malpighian tubules (Fig. 63) of the mosquitoes. Hu (1931) lists seven *Anopheles* spp., seven *Aedes* spp., and three *Culex* spp. as known hosts in which development is completed. The North American species are *Anopheles punctipennis, Aedes aegypti, A. canadensis, A. sollicitans, A. taeniorhynchus, A. vexans, Culex pipiens, C. fatigans, C. restuans,* and probably *C. salinarius.*

Dirofilaria magalhaesi is reported from man, one case in the left ventricle of a Brazilian child. Nothing is known of its development though, in all probability, mosquitoes serve as intermediate hosts. Faust *et al.* (1939) report finding a *Dirofilaria* (a male) from a native of New Orleans, naming it *D. louisianensis.*

ENCEPHALITIDES

A number of virus diseases have been generally grouped under this title. Of these virus diseases mosquitoes have been definitely proved as vectors of equine encephalomyelitis (eastern and western strains in the United States and Canada and Venezuelan strain in Trinidad and northern S. America), St. Louis encephalitis (in middle and western United States), Japanese B encephalitis (Japan, Formosa, maritime area of China, and probably Siberia).

EQUINE ENCEPHALOMYELITIS: This disease has long been known, under various names, as a highly fatal disease in horses. Meyer *et al.* (1931) first isolated the virus from sick horses in the San Joaquin Valley, California. In recent years thousands of horses in the United States have suffered from this disease (nearly 400,000 in the years 1935 to 1939) and many also in western Canada; the death rate varied from 30 to 90 per cent. In 1938 during an outbreak of equine encephalomyelitis in Massachusetts human cases developed and were definitely established as caused by the virus of equine encephalomyelitis. In the same year human cases were also diagnosed in California. It is now established that in North America there are two strains, the western strain (occurs west of the Appalachian Mountain ranges) and the eastern strain (east of those mountains). Sporadic human cases were reported from various sections of the United States from 1938 till the great epidemic of 1941, when over 3000 human cases occurred in North and South Dakota, Minnesota, and the Canadian provinces of Manitoba and Saskatchewan (545 cases in this last province alone). From the beginning mosquitoes were suspected as vectors owing to their abundance and prevalence at the times and places of the outbreaks. Experimentally *Aedes aegypti* was shown by Kelser (1933) to be easily infected by the western strain if fed on guinea pigs within two to three days after inoculation; there was an incubation period in the mosquito of at least six days. Soon a considerable number of mosquito species were shown experimentally to be capable of transmitting the disease, and the virus was shown to multiply in the mosquitoes. During the great human outbreak (1941) *Culex tarsalis* Coq. was found naturally infected in the Yakima Valley, Washington, by Hammon *et al.* (1941). Since then the following mosquito species have been found naturally infected:

Species	*Disease*	*Distribution and habits*
Culex tarsalis Coq.	Western strain (many times); St. Louis encephalitis	West of the Appalachian Mountains; breeds in all sorts of ground pools, containers; feeds on birds, man, etc.
Culex pipiens Linn.	Western and St. Louis encephalitis	Widespread; breeds as above; feeds readily on birds, man.
Culiseta inornata Will.	Western strain	Widespread; breeds in more or less permanent woodland pools; bites man.
Anopheles freeborni Aitken	Western strain	Western N. America, west of the Rocky Mts.
Aedes dorsalis (Meig.)	Western strain	Widespread in northern U.S.; pool breeder, fresh or saline; bites man.
Mansonia perturbans (Walk.)	Eastern strain	Widely distributed, bites man. Found infected in Alabama. (Personal communication)

At the present time no species of mosquito has been found naturally infected with the eastern strain. Experimentally the following species have been shown capable of transmitting either the western or eastern strain: *Aedes aegypti* (both strains), *A. sollicitans* (both strains), *A. nigromaculis* (western), *A. dorsalis* (western), *A. taeniorhynchus* (both strains), *A. vexans* (both strains), *A. cantator* (eastern), *A. triseriatus* (eastern), *A. atropalpus* (eastern). In addition the tick, *Dermacentor andersoni* (western strain, transmission and transovarial transmission), the mite, *Liponyssus sylviarum* (western strain, natural infection in California), the chicken mite, *Dermanyssus gallinae* (western strain, natural infection), and the bug, *Triatoma sanguisuga* (strain ?, in Kansas) can transmit one of the strains.

Venezuelan equine encephalomyelitis appears to be quite similar to the eastern strain of North America. Recently human cases have been reported from Trinidad. Gilyard (1944) reports the mosquitoes *Aedes taeniorhynchus, Anopheles neomaculipalpis,* and *Mansonia titillans* to be natural vectors.

St. Louis encephalitis appears to be a strictly neurotropic virus. In 1933 and 1937 extensive outbreaks occurred in St. Louis and the surrounding county. The virus was isolated in 1933 and proved to be a new virus. The outbreak of 1933 involved over 1000 human cases. The disease has now been reported from various parts of the western half of the United States. Hammon *et al.* (1941) isolated the virus from wild *Culex tarsalis* (captured in the Yakima Valley, Washington). This mosquito is known to be a definite vector. *Culex pipiens* has also been shown to be a vector. Smith *et al.* (1944, 1945, 1946, 1948) have proved that *Dermanyssus gallinae* (the common chicken mite) is a natural vector among poultry and that there is transovarial transmission through generation after generation. This mite seems to be the natural reservoir of the virus, infecting poultry and maintaining the disease. From infected birds mosquitoes obtain the virus and transmit it to other birds and animals, including man. In addition, the dog tick, *Dermacentor variabilis,* can transmit the virus in all stages and also through the egg. Hence this tick may also prove a good reservoir. The following mosquitoes have been shown capable of transmitting the virus of St. Louis encephalitis under experimental conditions or they have been found infected in nature: *Culex pipiens, C. quinquefasciatus, C. tarsalis, Aedes aegypti, A. dorsalis, A. lateralis, A. nigromaculis, A. taeniorhynchus, A. triseriatus, A. vexans, Anopheles freeborni, A. punctipennis, Culiseta incidens,* and *C. inornata.*

Japanese B encephalitis has been known from about 1871. In 1924 an extensive outbreak occurred in Japan and since then numerous cases have been recorded from those islands. Hsiao and Bohart (1946) report 12,341 cases between 1924 to 1933 with a death rate of 64.8 per cent. The disease has also been reported from Okinawa, where cases occurred among American troops as well as natives. From all available evidence mosquitoes are the vectors, and experimental transmission has been accomplished with *Culex pipiens pallens, Culex tritaeniorhynchus,* and *Aedes togoi.* In *Culex pipiens pallens* there was successful transovarial transmission. The last species and *C. tritaeniorhynchus* were found infected in nature.

RESERVOIRS OF ENCEPHALITIDES: It has been well established that the reservoirs of the eastern and western strains of equine encephalomyelitis and St. Louis encephalitis are primarily birds, especially domestic poultry. It will be noted that the mosquitoes concerned in the transmission of these diseases are well-known feeders on birds and also on man. Among birds the disease is undoubtedly transmitted by these mosquitoes, though the chicken mite, *Dermanyssus gallinae,* has been shown to be a most efficient transmitter among domestic fowls. The reservoir of the other one does not seem to be known.

Rift Valley fever is a disease apparently restricted to parts of East Africa, particularly Kenya and Uganda. The virus of the disease was isolated in 1931, and in 1933 Daubney and Hudson demonstrated that mosquitoes (*Mansonia* spp.) were capable of transmitting the virus by inoculation (experimental). The disease occurs principally among sheep and cattle though goats, mice, and rats are susceptible. Monkeys are also known to be susceptible. During an outbreak in Kenya in 1944 humans, principally shepherds, became infected and laboratory personnel are reported to have contracted the disease. Smithburn *et al.* (1948) recovered the virus from a number of mosquitoes caught in the wild in Uganda. They report *Aedes tarsalis* Newstead, *A. albocephalus* Edw., and *A. dendrophilus* Edw. to be naturally infected. However the females of the first two species are not easily differentiated with certainty. *Eretmapodites* spp. were recovered infected in the wild several times, and E. *chrysogaster* Graham was shown to transmit the disease experimentally.

MYIASIS (See Chapter XVII)

Certain species of mosquitoes act as mechanical carriers of a human- and animal-myiasis-producing fly, *Dermatobia hominis.* For a full account see pages 517–521.

BIRD MALARIA

Species of the genus *Culex* are responsible for the transmission of bird malarias, rather common and widespread diseases of birds.

FOWL POX

Fowl pox, a common and widespread disease of poultry, has been shown (1928–1931) by several workers to be transmitted by a number of different species of mosquitoes.

REDUCTION IN LAND VALUES

It is common knowledge that an abundance of mosquitoes causes a marked reduction in land values. This is particularly true in summer, seaside, and lake resorts and in urban areas subject to mosquito invasion. Manufacturing and industrial districts often feel the effects of mosquito abundance. Some of our most valuable lands as in New Jersey and the bottom lands of Mississippi have had and continue to have their development retarded owing to hordes of mosquitoes, which frequently render life, except to the most hardened, unendurable. When this is accompanied by diseases, the development is almost stopped. Furthermore, outbreaks of malaria and dengue throw another heavy burden on such communities due to sickness, the consequent loss of income, and the expense attendant thereto. The remarkable results following mosquito control and the consequent increase in real estate values and the health and vigor of the peoples have been noteworthy in many places but only a few can be cited, as Havana, Panama, the Canal Zone, Port Said, and Singapore. Where diseases are not present, but only noxious mosquitoes, the reduction of the latter brings about a marked increase in land values. No finer example can be cited than the work done in New Jersey. Headlee (1926) after presenting a detailed summary of the tax valuations of the Atlantic and Bay Coast area of New Jersey for the past twenty-five years concludes with this remarkable statement, "Thus it appears, under New Jersey conditions, that, where salt-marsh mosquitoes are naturally absent, there has occurred an average increase in taxable values during the past ten years of 55 per cent more than where they are still present or only recently reduced; and that, where salt-marsh mosquitoes have been largely eliminated during the last ten years, there has occurred an average annual increase of 75 per cent more than where they are still present or very recently reduced."

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CHAPTER XII

The Problem of Mosquito Control

THE preceding chapter has outlined briefly the important relations of mosquitoes to human welfare. Though these have been known for many years, only recently have somewhat adequate measures been taken to reduce mosquito abundance and then mainly in the control of disease-transmitting species. This is exemplified in the great antimosquito campaigns where special diseases had to be controlled in order that certain national developments could be undertaken or that wars could be prosecuted. The results of such undertakings have been of unprecedented success. Witness the work in the Malay Peninsula, Cuba, the Panama Canal Zone, New Jersey, parts of California, Italy, parts of Greece, Palestine, Singapore, the Tennessee Valley, and recently in the conduct of the Second World War and in the proposed extermination of malaria in the United States. All of these vast control operations have been organized by able men supported by governments or private capital in order that epidemic diseases might be brought under control so as to permit certain national developments. Yet despite this, vast areas of the most fertile regions of the world suffer from mosquito-borne diseases which retard and, in some cases, prevent their agricultural and industrial development. Hoffman (1916) made a plea and presented a tentative plan for the eradication of malaria throughout the Western hemisphere. His plea was based on the knowledge "that malaria is perhaps the most important of human diseases, and though it is not often directly fatal, its wide prevalence in almost all warm climates produces an enormous amount of sickness and mortality." Boyd (1930) designates malaria as "the worst of human scourges"; Russell (1943) estimates that even today there are 3,000,000 deaths each year from malaria and at least 300,000,000 cases of malarial fevers annually throughout the world.

The problem of mosquito control may be considered from two viewpoints. First is the reduction and control of species known to be good vectors of disease—that is, *species control* or eradication. This is well illustrated by the work on yellow fever (urban) where the adequate control of *Aedes aegypti* will bring about the reduction and elimination of the disease. This, however, does not apply to jungle yellow fever, as we do not yet know all the complexes involved in control of this disease in jungle areas. Species control is also practical for dengue, for when *A. aegypti, A. albopictus,* and *A. scutellaris* are brought under control the disease usually disappears. This same procedure frequently applies to malaria. In our own country the control of *Anopheles quadrimaculatus* would mean the elimination of malaria in our eastern and southern states provided no new vector reached our shores. An adequate demonstration of this procedure is well illustrated by the great reduction of malaria in parts of northeastern Brazil by the control and eradication of the introduced vector *Anopheles gambiae.* Many more examples could be given of the effectiveness of this procedure in controlling human disease by controlling the vector, or by what is called "breaking the chain" in the life cycle of the parasite or virus. However, in the case of encephalitides, as St. Louis encephalitis, eastern and western encephalitis, etc. the control of specific vectors is not easily possible, not only because we do not know all of them, but because it would be difficult to conduct a campaign directly against those we do know. So another procedure should be considered. In planning the control of a vector of a disease it should be decided whether all pest mosquitoes ought not also to be taken into account. When an insect-borne disease is prevalent, it is usually not difficult to arouse public opinion and obtain funds for adequate control work. When the epidemic subsides the control operations are generally discontinued and mosquitoes breed in abundance to plague the inhabitants. If full information in such a campaign is given that all mosquitoes should be controlled in order that the inhabitants may enjoy freedom from mosquitoes as well as the disease, the good work can continue. This would increase the well-being of all and adequately provide against a future epidemic of the disease.

In many sections, not only of our own country but in various parts of the world, a wise, well-organized, well-directed plan of mosquito (and of flies and other pest) control by cities, towns, counties, or other units would bring about a gradual reduction of these noxious insects, prevent the outbreak of disease, reduce or eliminate malaria, permit people to enjoy their gardens, playgrounds, parks, or other recreation facilities and so increase land and real estate values that the actual cost would be more than repaid by the increase in taxable values. In planning such work several fundamental facts must be borne in mind. In the first place, water should be considered one of the first essentials in any community and the proper handling of such a valuable and essential natural resource must be given first consideration. It is easy to eliminate mosquito breeding if we eliminate all standing water, but such effective drainage might do more harm than good. How then shall such a problem be solved? In planning a control problem the area in which operations are to be conducted should be thoroughly studied and the following basic knowledge obtained:

1. The mosquitoes breeding in the control area should be determined and all breeding places definitely located.

2. The mosquitoes breeding outside the control area and that are liable to migrate should be investigated. This need not be an intensive survey but it should be careful enough to avoid sad experiences later when control activities are under way.

3. Topographical or aerial maps of the area should be obtained, and all mosquito-breeding places as well as all water areas such as ponds, wells, streams, lakes, and swimming pools should be carefully located on such maps.

The three steps stated above are essential to the outlining of control activities. How can they be carried out? Successful control depends on scientific knowledge. Mosquitoes, either in the adult or larval stages, can be identified only by those who know them—not by those who think they know them or believe that all mosquitoes have the same habits. In carrying out the first step much data may be obtained on breeding areas that can be located on the topographical map. But omitting all factors but the first one for the present, let us see the problem in its true relation to control. The species that is mainly responsible can usually be collected during an outbreak. If it proves to be the common house mosquito, *Culex pipiens,* the types of breeding grounds are well known, and certain control measures are indicated. If it proves to be *Aedes vexans,* a different breeding ground is assured, and other control measures must be applied. If the main outbreaks are due to the early spring species, as *Aedes stimulans, A. excrucians,* and *A. fitchii,* another type or types of breeding places must occur in or near the area. If anophelines are present in numbers, then still other types of breeding grounds prevail and other methods of control are indicated. If the main outbreaks are due to such migratory forms as *Mansonia perturbans, Aedes vexans, A. sollicitans, A. cantator,* or *A. taeniorhynchus,* the problem becomes more complicated.

The second step is necessary in order that the species breeding in the area surrounding the district under control may be known. If migratory species breed here, steps will have to be taken to reduce the breeding areas as much as possible.

The third step may be combined to a great degree with the first if determinations are made from the larvae. Every part of the area should be carefully mapped; all standing water, streams, ponds, cisterns, wells, catch basins, marshes, or lakes should be accurately located on a large-scale map.[1] All such places, particularly the ponds, streams, bayous, swamps, etc., should be carefully described so that changes of personnel will not delay the work.

When the above information is at hand, a definite plan for the ultimate reduction and elimination of breeding grounds may be undertaken. Any plan will depend largely on local conditions, the extent and character of the breeding grounds, and the species of mosquitoes involved. The only known methods now available are drainage operations, filling and grading, keeping the banks of streams and large ponds clear of marginal and floating vegetation, employment of surface-feeding fishes, oiling operations, and the use of poisons or the new remarkable insecticide, DDT. Any plans evolved should be in co-operation with all the other agencies which have to do with sanitation, city or rural planning commissions, departments of public works, etc., and such work should be under the immediate direction of the agency dealing with public health. It is too early yet to hope for states or provinces to undertake large-scale operations unless it is in particularly malarious regions and then only in co-operation with national governments. When the co-operation of all public bodies and the citizens of a given area can be obtained, plans should be carefully prepared and continuity of activity is essential from year to year.

TYPES OF CONTROL OPERATIONS

When a plan for mosquito reduction suitable for the area under consideration has been evolved, particular attention should be paid to the various methods of control. A few of these may be briefly outlined here.

DRAINAGE

When the known breeding areas are fairly well determined in a given district, those that can be drained or greatly reduced by drainage should receive the most careful consideration. Plans for drainage should be made by expert sanitary or drainage engineers. Careful attention should be paid to the type of drainage, as open or closed drains, the grade of drainage, and the discharge of the flow. Where water has to be discharged from a diked tidal area, gates must be provided to prevent all backflow. This is true only if the land is to be reclaimed for agricultural or other developmental purposes. Otherwise open ditches with clean margins will permit the flushing of these areas at each high tide. If the drainage is well done, all water will be carried away within a few days and thus prevent a brood of mosquitoes reaching maturity. Furthermore, the inflow of the tides will bring an abundance of fishes, which will aid in devouring any mosquito larvae present along the drains or that hatch with the presence of water. The problems of salt-marsh drainage, diking, pumping, and the maintenance of ditches, are all very difficult, but exceptional progress has been made in New Jersey and California. In the interior, where discharge into rivers, bayous, or lakes

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[1] Such maps can be obtained by enlarging the topographical maps of the Geological Survey or aerial maps.

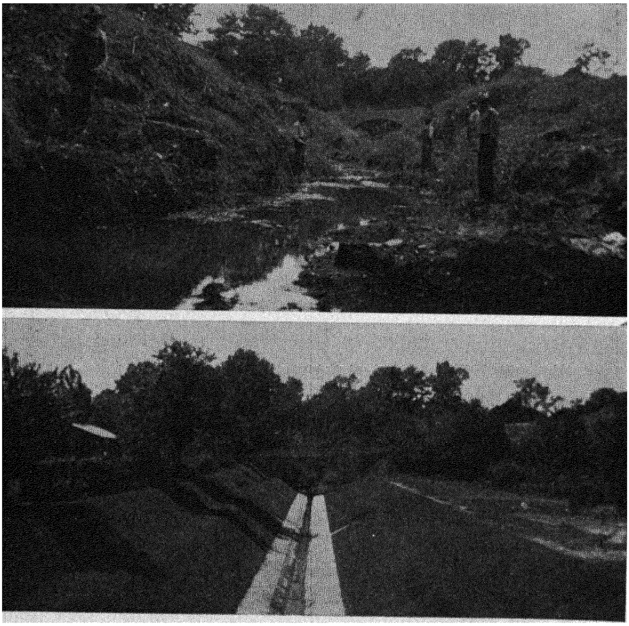

Fig. 138. Vicksburg, Mississippi. *Upper:* Before malaria control drainage. *Lower:* After construction of reinforced concrete invert with sodded banks. (Courtesy Mr. Rector and Mississippi State Board of Health.)

subject to rise in levels takes place, drainage gates should be installed. Various types are on the market, and full information can be obtained from engineering firms.

Drainage should be carried out only by experts. If well and carefully done (Fig. 138), the value of reclaimed lands, either for agricultural, developmental, or industrial purposes, will often more than repay the original cost. All drainage work must be carefully inspected from time to time in order that it be kept functioning properly.

FILLING AND GRADING

Filling and grading operations should be developed as a continuous procedure. Plans for this work can be made only when the mosquito-breeding areas are rather definitely located, and the work should be done in cooperation with whatever organizations have supervision of public works—park commissions, town- or city-planning commissions, building commissions, etc. In this way all temporary pools; stagnant and unsightly ponds; borrow pits; pools formed along railway embankments, by road or street construction, by building operations of all kinds, and by the impounding of water for city water supplies; and all operations of whatever kind that may bring about standing or stagnant water will be brought under the supervision of those in charge of mosquito-control work. By careful coordination of these various activities new ponds or pools may be avoided, and many old ones can be filled with the minimum amount of labor and cost. This feature of mosquito-control operations is one of the most important in cities, villages, and towns. Full authority by law should be provided for carrying out effectively the sanitary regulations involved in any or all such operations.

STREAMS AND PERMANENT PONDS

Local streams, rivers, and permanent and impounded bodies of water present many difficulties. Where the streams are sluggish and the banks have marginal vegetation, with little side pools, bayous, bottom lands subject to overflow, etc., the problem becomes complicated. As far as possible, the stream should be diverted in a direct course with the maximum amount of fall. The vegetation and shrubbery should be removed but not so as to give an unsightly appearance. All rocks and debris that prevent a free flow or may provide stagnant pools during drought should be removed. Bottom lands subject to flood may be drained by subsoil drains. The control work along streams and rivers should be made as permanent as possible.

In the case of large ponds or reservoirs that must not be drained, it is possible to reduce and even prevent mosquito breeding. Such bodies of water should have clear margins; the trees and shrubbery should be removed for some distance from the banks; flotage and the growth of all types of floating vegetation should be prevented (Fig. 139). This will allow free wind action, which will largely prevent oviposition; the removal of the shrubbery destroys the resting and hiding places for the adults. This method of procedure has been found quite successful in some sections of Louisiana where stagnant water in bayous has been impounded by damming, raising the water level, clearing out debris, and removing the shrubbery. Here it was not possible to drain as the river level was higher than that of the bayous and pumping

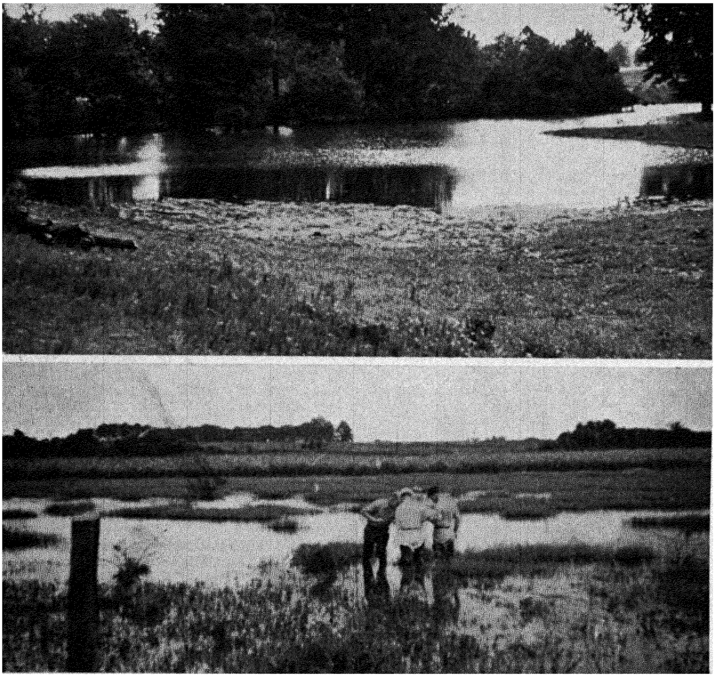

Fig. 139. Upper: A clean shore line where breeding of anophelines is practically eliminated. *Lower:* An area where it is practically impossible to obtain a clean shore line and breeding is abundant. (Wheeler Lake, Tennessee River.)

was not advisable, so the experiment of impounding these waters was tried and proved successful. This type of water storage should be attempted in other sections of the country.

Local conditions create special problems, but as our knowledge of mosquito biology increases, methods may be devised to prevent or control breeding. In many parts of the tropics the most hopeless situations have been valiantly attacked, and the results have been successful beyond the fondest hopes. It would therefore appear that even the most difficult situation in America can be successfully attacked if we have the courage and perseverance to push on to the end.

IMPOUNDED WATERS

The problem of mosquito control, particularly of anophelines that are active vectors of malaria, in areas where there has been extensive impoundage of water for power, flood or erosion control, or fish ponds has become a major one in many parts of the world as well as in our own country. Here the problem of water management is of great importance. Kiker and Stromquist (1939) have laid down the essential requirements in the preparation of a reservoir for impoundage: "That the reservoir be cleared so as to present a clean water's surface after impoundage between maximum and minimum water levels; and that all depressions between maximum and minimum water levels be drained so as to provide water level fluctuation with the reservoir." When water is impounded in this manner, the problem of anopheline control is greatly simplified. In addition to the usual control measures, outlined in the next few pages, a system of fluctuating water levels will show marked results in the reduction of mosquito breeding. During the breeding season the water level is lowered at regular intervals and then raised to within an inch or more of the previous level. The period of each fluctuation is usually about a week. This procedure may be called "cyclical fluctuation with water-level recession." By this method shore-line debris is stranded and marginal vegetation is largely prevented from gaining a foothold. The problems of marginal vegetation and debris are most important since such protected areas are ideal places for mosquito breeding. Until more is learned of the biology of shore-line aquatic and semiaquatic plants not much further progress can be made in the management of shore-line problems. The only thing that can be done on the basis of our present knowledge is to maintain clean shore lines (Fig. 139) by every available means as well as by water-level fluctuation and recession.

When feasible it has been found advantageous to maintain high water levels, above the maximum "mosquito control" elevation, at the beginning of the growing season in order to delay the development of marginal vegetation. This constant-level phase should be maintained until significant anopheline production begins. Such a procedure will prevent the seeds of some objectionable plants from gaining a foothold in the marginal areas and thus give a cleaner shore line later in the season when anopheline production is at its maximum.

OILS AND OILING OPERATIONS

Kerosene oil was one of the first oils suggested and used for the killing of mosquito larvae. It is still used and is very effective, but the film formed on the water surface is soon broken down, especially in warm climates. At present various grades of petroleum oils are extensively used throughout the world. In order to act effectively an oil should have the following qualifications: (a) it should be highly toxic to larvae and pupae; (b) it should spread evenly and rapidly on all kinds of water; (c) it should penetrate through debris and vegetation; (d) it should form a fairly stable and lasting film; (e) it should be noninjurious to man and not kill fish, waterfowl, or plant life; and (f) its cost should be reasonable. Such an oil is not easily obtainable, and various types are employed to meet the conditions under which they are used.

How oils kill mosquito larvae is not very well understood. It is generally stated that the oil film is drawn into the tracheal system, and if the oil is of high volatility, the toxic action is very rapid owing to the penetration of the tissues. If the oil is of low volatility and viscosity, the death of the larvae and pupae is probably due to suffocation.

After extensive investigations and field trials the New Jersey Experiment Station recommends an oil with the following qualities: type—distillate fuel oil; gravity (A.P.I.)—27-33; flash—130° F. or higher; viscosity S.U. at 100° F.—35 to 40; distillation—10 per cent at 430°-450° F., 50 per cent at 510°-550° F., 90 per cent at 630° F. and higher. This oil spreads well, will give a practically perfect kill of larvae and pupae within a few hours after application, and leaves a fairly stable film. Under normal conditions the film will not last more than ten days to two weeks. This requires that fresh applications be made whenever breeding is observed. The amount of oil required varies according to the breeding area and the vegetation present. Twenty-five to sixty gallons will usually cover any given acre of water surface.

Fuel oil as described above is rather objectionable on small ponds in private grounds, on fish ponds, on ponds containing aquatic ornamental plants, on ponds frequented by waterfowl, or in similar aquatic situations. To meet this objection the New Jersey Experiment Station devised a mixture of pyrethrum and oil known as the New Jersey Pyrethrum Mosquito Larvicide. It is composed of 66 per cent kerosene or similar light petroleum distillate; 0.07 per cent pyrethrins; 33.5 per cent water; and 0.5 per cent sodium lauryl sulfate. This is a stock solution and is diluted 1 part to 10 parts of water before using. It kills larvae and pupae promptly, is not injurious to fish, plants, or waterfowl, but does not give any lasting film.

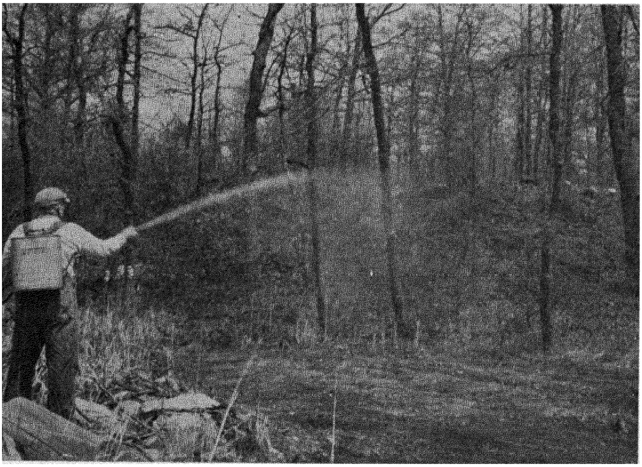

Fig. 140. A shoulder spray tank used in spraying small ponds. (Courtesy Connecticut Agriculture Experiment Station.)

In the Panama Canal Zone Curry (1943) reports most effective control of larvae and pupae by the use of ordinary bunker fuel oil as furnished by the United States Navy. The oil spreads well and kills promptly; the film is effective for about two weeks under the hot tropical sun. In general any good fuel oil is highly toxic to mosquito larvae. However, practically all these oils are not very effective on water heavily charged with sewage.

The time of applying oil is of great importance. In many sections of the country where the early spring species are the chief menace the oil must be applied before the adults have emerged. Many of these species have only a single brood each season; hence the control measures must be carried out at the proper time. In sections of the country where there are several to many annual broods or where different species breed at different times the timing of the oiling operations is very important. Oil films break down in a short time, rarely lasting more than ten days to two weeks. In cooler climates the oil film is effective longer than in hot climates. Severe rainstorms may also affect the oil film. Careful inspection is essential to determine the timing and effectiveness of the oiling operations.

The method of applying the oils will depend largely on the area to be covered, its accessibility to roadways, and the difficulties of actually reaching the water. On small ponds and streams, in wooded areas, in marshes, swamps, and similar places, the ordinary shoulder spray tank is most satisfactory (Fig. 140). Here the pressure is obtained by compressed air, and any size of nozzle may be used but preferably one that gives a fine mistlike spray. In areas accessible to trucks, as along roadways, extensive narrow marshes, or swamps, the oil may be applied from an auto truck having a tank and a pump driven by the engine of the truck (Fig. 141). Such power-driven spray outfits are in extensive use in orchards, parks, and woodland areas to control insect pests. They can easily be employed in antimosquito campaigns. By the use of several leads of hose, and lengthening them, extensive areas can be covered in a minimum time. Their use will depend entirely on local conditions and their availability.

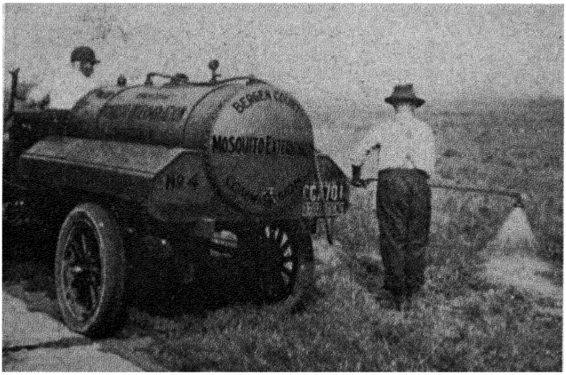

Fig. 141. A power sprayer used in oiling large areas accessible to roadways. (Courtesy Bergen County, New Jersey, Mosquito Commission.)

Many other methods of applying oil have been tried and some are in use. Streams, ditches, and ponds have been treated by placing barrels filled with oil above them, the barrels being so constructed that a constant drip reaches the surface of the water. The oil is gradually carried onward by the stream or spreads slowly over the surface. This is not very satisfactory owing to the failure of the oil film to penetrate the grassy margins, drift, or flotage. Waste soaked in oil and anchored in ponds has the same drawbacks. Fine sand soaked in oil and sowed broadcast over ponds has given satisfactory results. As the sand falls on the water or sinks through the vegetation to the water surface, the oil is given off and leaves a good film.

In large lakes, ponds, and reservoirs, where the margin and flotage is not easily accessible except by small boats, a tank placed in a boat and fitted with a pump to give the necessary pressure may be employed (Fig. 142). The pump may be used to force the oil out directly or it may be used to compress the air. If air compression is employed, pumping is not continuous and in general a better and more even spray may be obtained.

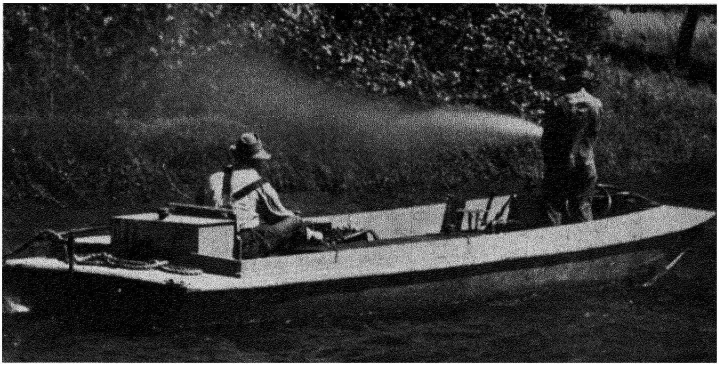

Fig. 142. Spraying a shore line with a petroleum oil mixture for mosquito control from a power boat. (Courtesy Tennessee Valley Authority, Division of Health.)

In all oiling work the most essential points are the use of a good, free-running, toxic oil, good equipment, and extreme care in covering all the water surface with a film of oil. The laborers should be carefully trained and their work constantly supervised by reliable inspectors.

POISONS

In recent years poisons have been used extensively for the control of anophelines. As the larvae are surface feeders, any poison that will remain at the surface or on the surface film for a short time will be eaten by them. In this work Paris green has been found most efficient and has been employed extensively in areas where malaria is endemic. The Paris green is diluted with a diluent such as soapstone, hydrated lime, or road dust and dusted on the surface by various means. When well done, the results are almost perfect, destroying practically 100 per cent of the anopheline larvae. More recently airplanes have been employed, which, carrying specially designed apparatus, have dusted large areas of marshes, swamps, densely wooded areas, lakes, and reservoirs with the greatest success. Only a pound to a pound and a half of Paris green need be used per acre. The most important problems in this work are to determine the correct diluent and the particle size of the Paris green in order that the dust may settle promptly and remain for some time on the surface film. In dusting either by hand or by airplane the work must be done when there is no wind, usually in the early morning hours, or much of the material will be lost. Furthermore the pilots must be trained for low flying, 20 to 50 feet above the water surface (Fig. 143). As yet no successful way has been found to destroy the larvae of culicines by poisons, though much experimental work has been directed to this end.

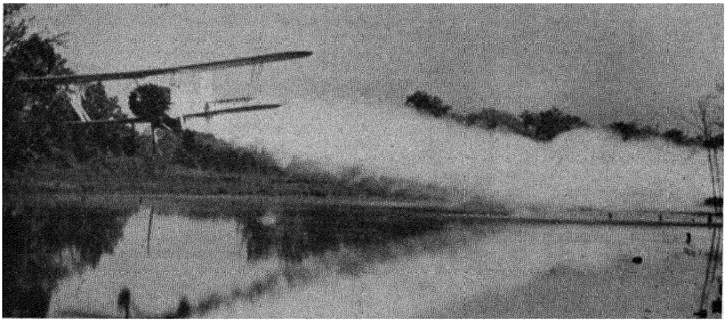

Fig. 143. Airplane dusting with Paris green for the control of *Anopheles* larvae. (Courtesy Tennessee Valley Authority, Division of Health.)

Recently it has been shown that borax, in concentrations of two to two and a half ounces per gallon of water, is effective in preventing mosquito breeding in rain-water barrels, cisterns, and similar containers. Borax-treated water should not be used for drinking purposes. It is excellent for washing purposes. The advantage of borax over oil is that it is permanent and needs only to be renewed when the cisterns, etc., are refilled by fresh water. Water barrels so treated have remained all summer without further treatment. It is only necessary to add more borax when the barrels are refilled by fresh rain water.

Many other substances are under investigation, such as derris, pyrethrum powder, and other arsenicals, and methods of employing them against the non-surface-feeding culicines will undoubtedly develop.

DDT AS A LARVICIDE

During the Second World War a new insecticide appeared and received deserved attention. This is DDT or dichloro-diphenyl-trichloroethane or as 2,2-bis (*p*-chlorophenyl) -1-1, 1-trichloroethane. It is a white crystalline solid and was first produced in 1874 by Zeidler, a German chemist. Its melting point is 108° to 109° C (226.4° to 228.2° F.). It is practically insoluble in water but dissolves in many organic solvents as the following:

Solvent	*Grams DDT in 100 cc. solvent*
Cyclohexanone	100 to 120
Benzene	77 to 83
Xylene	56 to 62
Acetone	50 to 55
Diesel oil No. 2	10 (approx.)
Kerosene, crude	8
Kerosene, refined	4
Velsicol	20+

DDT has been experimented with in various forms by many workers in the United States, in war areas, and in other parts of the world. At present the following methods may be employed:

1. A 0.5 per cent DDT in refined kerosene (water white) or Diesel oil No. 2 at the rate of 0.05 pound per acre gave good control of larvae in Tennessee Valley Authority experiments. This would mean the application of about 1.3 gallons of the mixture per acre. This preparation would require 4 pounds of DDT (pure) or 20 pounds (20 per cent DDT) to each 100 gallons of kerosene oil and it should be applied at the rate stated above. A 5 per cent petroleum oil solution may be prepared by dissolving 2⅛ pounds of DDT in 5 gallons of No. 2 fuel oil or kerosene oil. For treatment use only at the rate of 2 quarts per acre of water surface. The spray must be applied as a fine mist with slow delivery.

2. A wettable DDT powder containing 50 per cent DDT could be used in the same proportions in ordinary water. This would require 8 pounds of the powder to each 100 gallons of water, but it should probably be applied at a higher rate as 2 to 5 gallons per acre. For culicine larvae these dosages should be increased about 2 times or slightly more. This form of DDT is usually referred to as a suspension.

3. Water emulsions are prepared by dissolving DDT in one of the solvents

and adding a wetting agent or emulsifier to form a concentrate. One of the concentrates recommended is 25 pounds of DDT and 4 pounds of Triton X-100 in 71 pounds of xylene. Dilutions are made by adding the required amount of the concentrate to water slowly, with continuous stirring. A 5 per cent emulsion of DDT is prepared by adding 1 volume of the concentrate to 4 volumes of water or 1 volume of concentrate to 24 volumes of water for a 1 per cent emulsion and so on. As emulsions mix promptly with water, the effect of DDT on other aquatic organisms as Crustacea, fish, and aquatic insects other than mosquito larvae may be detrimental. At present the allowable amount of DDT to prevent damage is about 0.1 pound per acre of water surface. This would mean using about 2 gallons or less of a 1 per cent emulsion per acre so as not to exceed 0.05 p.p.m. of DDT in the water. In cisterns, wells, urns, or other containers the water of which is not used for drinking purposes the dosages should be increased to double or more and thus give more lasting control.

4. DDT as an aerosol is handled by airplanes adapted for atomizing an oil solution of DDT. The solution (20 per cent DDT in Velsicol NR-70 as employed by the Tennessee Valley Authority) is carried in the plane (Stearman 17), and by means of pumps it is forced into a pipeline from the engine exhaust line (4-inch pipe) just in front of a standardized venturi so as to give a mistlike spray with droplets of 25 to 50 microns in size. By using such standardized equipment an effective swath of 200 feet wide could be covered each trip by the plane, and this would give effective control (about 90 per cent larval kill). The amount applied at each treatment was 0.1 pound per acre of water surface. Sixteen routine treatments in a single season over the same area gave excellent control of mosquito larvae and had no appreciable effect on fish food organisms (though most surface Hemiptera were destroyed). However, good results have been obtained by applying as little as 0.05 pound per acre of water surface.

5. Many successful attachments for spraying DDT have been developed for various types of planes. For ordinary routine work involving considerable areas the Stearman 17 and various types of Army and Navy planes have proved very effective. The spray is delivered under pressure of about 100 pounds per square inch by means of a pump and is delivered through a breaker bar placed on the underside of the lower wing on each side. Along each breaker bar are located a varying number of spray nozzles of the proper type to give the desired spray coverage.[2] Using such a plane a large area can

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[2] The breaker bar has recently been largely replaced by a system of atomizing nozzles located along the trailing edge of the wings, or at outer corners of wings and tail.

be covered with a highly concentrated DDT solution in very small amounts. The amounts applied per acre varies, but good results have been obtained by applying as little as 0.1 pound of DDT per acre as sprays (0.2 quarts of a 20 per cent DDT solution).

DDT AS AN ADULTICIDE

The application of DDT solutions to the surface of buildings, both within and without, have given good results in killing adult mosquitoes and other insects. As a result of numerous experiments the desired deposit (residual) to give adequate kill is about 200 milligrams of DDT per square foot. This is obtained by using a 5 per cent DDT solution in kerosene oil (5 pounds of DDT in 12½ gallons of kerosene oil). To obtain a residue of 200 milligrams per square foot requires about 1 gallon of the 5 per cent mixture per 1000 square feet. In applying the material a fine, not a mist, spray is required, and it should be under a pressure of 40 to 50 pounds so as to cover the surface without any runoff. Such a deposit when well applied will give adequate kill for over a month or longer. Such deposits can be obtained by the use of hand sprayers, knapsack sprayers, or power sprayers so long as adjustments are made to leave the proper amounts. This type of anopheline control has shown good reduction of malarial incidence in areas where extensive spraying of all buildings (on the inside) has been undertaken. More recently the wettable DDT suspensions have also given good kill of adults (mosquitoes and flies). The 50 per cent wettable DDT is usually employed only outside on gardens, shrubbery, trees, about bases of houses, and inside barns, chicken houses, and similar buildings. The wettable DDT gives good results when applied indoors at concentrations of 5 to 12 pounds in 50 gallons of water, but usually leaves undesirable deposits in private homes.

Aerosol bombs have been employed for some time for the killing of adult mosquitoes and flies. These bombs, in various sizes, are on the market and full directions for their use are stamped on each bomb.

DDT FOR THE DESTRUCTION OF HIBERNATING ADULTS: Not much work has been done in this field owing to the difficulty of determining the main places of hibernation. However, Aitken (1946) describes such a treatment in an area of some 93 square miles in Italy. All the houses, barns, outbuildings, and places of shelter were thoroughly treated so as to give about 83 milligrams of DDT per square foot. The results indicated a marked decrease in anopheline breeding the year following treatment. There was also a recession of malaria from a splenic index of 43 per cent to 25 per cent and a parasitemia from 21 per cent to 1 per cent. In an area where no such treatment was given the malaria index showed a marked increase. Soper *et al.* (1947) indicates somewhat similar results from the treatment of all buildings, etc., in an area of 120 square miles in the Tiber Delta, Italy. They used 6.5 per cent DDT in kerosene so as to leave about 200 milligrams of DDT per square foot of surface. This method should prove of value in areas where the main hibernating places of the anopheline carriers are mainly buildings of the local inhabitants.

NATURAL ENEMIES AS CONTROLS

Mosquitoes have many natural enemies, both as predators and parasites. Certain species of birds, bats, and insects prey upon them, but their effectiveness in reducing the mosquito population does not appear very marked. Many species of fish feed on the larvae and certain top-feeding fishes (minnows, gold fishes, etc.) have been employed in attempts to reduce mosquito abundance. *Gambusia affinis* is probably one of the most valuable of top minnows as it is hardy, breeds rapidly, and normally frequents shallow water suitable for mosquito breeding. *Gambusia holbrooki,* a close relative of *G. affinis,* has been carefully studied by Hildebrand (1925) and his conclusions warrant the utilization of this species wherever it can be employed. His experiments covered a considerable range of aquatic environments, especially those with dense growths of water plants, and he found that *Gambusia holbrooki* brought about a very marked decrease in mosquito breeding. In no single instance was the control perfect, but in certain experiments the results almost approached complete control. *Gambusia affinis* is a native minnow of the great Mississippi Valley; *G. holbrooki,* native to the Atlantic watershed; yet, despite their present wide distribution and abundance, reliance on mosquito control by these fishes depends largely on introducing them into mosquito-breeding ponds, lakes, streams, etc., frequently each year. Furthermore, in order that the fishes may do effective work, dense growths of aquatic vegetation must be prevented. The maintenance of top-minnow hatcheries is not difficult so that the costs of fish control are not high. Though *G. affinis* has been introduced into many parts of the world and striking successes have attended its introduction, yet too much hope must not be placed on fish as effective agents in mosquito control. As a natural aid they are extremely valuable. Connor (1921) used, with remarkable effectiveness, the *chalaco* (*Dormitator latifrons,* family Gobiidae) in the campaign against yellow-fever mosquito in Guayaquil, Ecuador. Here the city had no adequate water supply, the water being distributed daily to the householders and stored in tanks, cans, and other receptacles. As there were over 7000 tanks and 30,000 other types of water receptacles, the breeding of *Aedes aegypti* continued in great volume. As a modern water service could not be installed at once, Connor conceived the idea of using fish. After many trials he selected the *chalaco* and distributed at least one fish for every container. The fish, a local species, was obtained from fishermen and stored in a specially prepared well where conditions approximated those of the streams from which the fish came. In a few days the fish were transferred to a second well containing water similar to that used in the city. From the second well the fish were distributed to all water containers throughout the city. The results were remarkable, for mosquito breeding was reduced to a minimum.

Many other species of top-feeding fishes have been employed and with considerable success. Though undoubtedly fishes play an important role in mosquito reduction and the utilization of certain species is highly to be commended, yet adequate control cannot be obtained by them alone unless the conditions are more or less ideal from the standpoint of the fishes employed. In any plan to use fishes in a control area, the best possible scientific advice should be obtained. The effectiveness of the fishes depends on conditions which bring about their rapid breeding and maintenance and furnish them a continuing food supply.

OTHER METHODS OF MOSQUITO REDUCTION

In recent years much attention has been devoted to the study of the aquatic conditions that favor or reduce mosquito breeding. It is a common observation that certain ponds, etc., are favorite breeding grounds while in other similar ponds or marshes no breeding occurs. Though much work has been done, no definite conclusions seem warranted. Certain aquatic plants as *Chara* and *Phyllotria* species appear to have a deterrent effect both on egg deposition and larval development. Other plants, as *Utricularia* spp. (Fig. 144, bladderworts) destroy large numbers of larvae (Matheson, 1931) though Hildebrandt (1925) concluded that *U. macrorhiza* (= *vulgaris*) and *U. radiata* had very little effect in reducing larval abundance in ponds that he observed in the southeastern states; surface-loving plants as species of *Lemna, Wollfia* (Fig. 144), and *Azolla* form dense mats on the water surface and prevent egg deposition or interfere with larval development; and other plants may play important roles in the prevention of breeding or encourage excessive abundance of larvae. In general it may be said that the presence or absence of the necessary larval food appears to be the deciding factor. But what is the necessary larval food? Many examinations of the larval gut contents have been made; some studies of the plankton in typical breeding pools versus nonbreeding pools have been carried out; from these, however, no conclusions can yet be drawn. As the larvae sweep all available material into their intestinal tracts, there is no means of deciding what is actually digested and what is passed out in the wastes. Hinman (1930) has shown that a large proportion of the material ingested by the larvae passes through the alimentary canal unchanged and thus cannot be regarded as food. He further demonstrated that larvae of *Aedes aegypti* can be reared under sterile conditions. Eggs, sterilized externally, were introduced into Berkefeld-filtered water, and normal adults emerged in eight to nine days (the usual time under the most favorable conditions). The only food available for these larvae was the solutes and colloids that could pass through the finest filters. Matheson and Hinman (1931) also demonstrated that larvae of several other species of mosquitoes grew vigorously in Berkefeld-filtered water. It would seem clear, then, that probably the most important sources of foods for mosquito larvae are the substances in solution and colloids present in the water. If we could

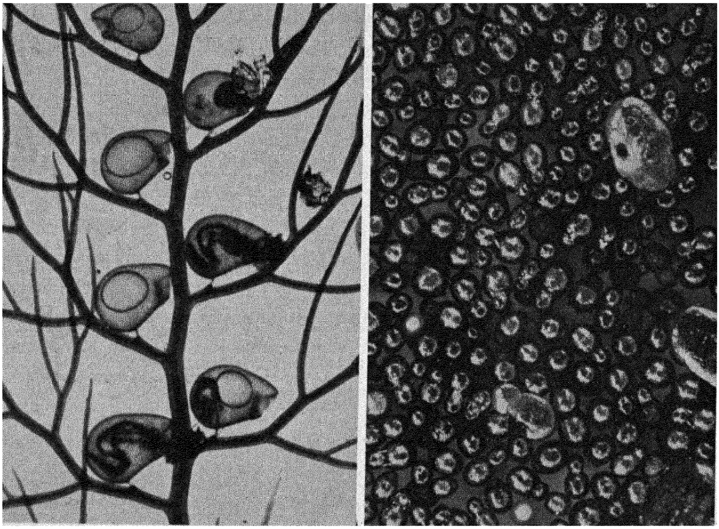

Fig. 144. Left: Portion of stem of bladderwort (*Utricularia*) with mosquito larvae in four bladders. *Right:* Surface of water completely covered by *Wollfia punctata* and a few plants of *Lemna minor.*

determine what are the essential solutes, considerable progress might be made in simplifying the problem of mosquito control. If by the use of certain aquatic plants, by the chemical treatment of water areas, etc., the necessary larval food can be destroyed, mosquito control operations may be greatly simplified and rendered less expensive.

PROTECTION FROM MOSQUITOES

SCREENING

Though actual control measures against both larvae and adults of mosquitoes may be carried on in any locality, probably the most effective measure to ensure comfort in homes is by screening. Screening not only effectively bars mosquitoes but also eliminates many other noxious insects as houseflies, black flies, and others. In all populated areas where financial means are adequate screening should be practiced. In areas where housing is poor, financial means are not available, and the population is indifferent, every effort should be made to aid such communities. It has been definitely proved that adequate screening, even in highly malarious rural areas with inadequate housing, will reduce malaria to a minimum. Screening should be well done so that no entrances are left, such as through open fireplaces or openings in flooring or walls. Porches should also be screened. Such screening combined with DDT treatments (residual sprays) of the interior and screens will ensure comfort in homes. The type of screening wire will depend largely on the locality and the availability of material. In general the 16-mesh screen (16 meshes to the inch) will prove most useful. Copper, bronze, or galvanized screens are available and recently plastic screens have been developed. Copper or bronze screens are long lasting, even in areas near the sea, while galvanized screens may give only a few years' service and then must be repaired or renewed. Full details of methods of screening will be found in the references.

PERSONAL PROTECTION

When traveling or living in areas where there are dangerous insect-borne diseases (malaria, yellow fever, filariasis, dengue, etc.) bed nets should be a part of the equipment. These are available or may be made. In entering a bed net great care should be exercised to see that all mosquitoes or other insects are absent or are killed. The bed net should be carefuly tucked about the bed or sleeping place so as to leave no opening, and the net should be so arranged that the sleeper's body does not touch the net at any point.

During World War II excellent mosquito repellents were developed and tested. These consist of Rutgers 612 (2-ethylhexanediol-1-3), dimethyl phthalate, and indalone. They are available and give a fair degree of protection against mosquitoes and black flies. For general protection against insects a combination of the three is recommended, i.e., 6 parts of dimethyl phthalate, 2 parts of Rutgers 612, and 2 parts of indalone (the so-called "6–2–2" formula). These materials should be applied according to the directions of the manufacturer. They are not injurious to the skin and should be rubbed over all exposed surfaces, but avoid getting them into the eyes. Alone or in combination they will give fairly good protection for two to four hours. They can also be rubbed or spread over the clothing with impunity and thus give added protection.

SPECIAL CONTROL PROBLEMS

The general methods of mosquito control have been outlined above. Several special phases need to be emphasized. These concern the control of yellow fever, malaria, and dengue. Though yellow fever is now known to be transmitted (at least from monkey to monkey and probably from man to man, or monkey to man) by many species of mosquitoes in addition to the yellow-fever mosquito (*Aedes aegypti*), the transmitter that must be considered of prime importance is the last one. Furthermore, an animal reservoir of at least vast possibilities has been discovered in a large number of different species of monkeys. At present the disease is restricted to extensive areas in South America and a large area in West Africa extending deep into the continent. Formerly it was thought that if the disease in man could be stamped out, either by the death of the infected or their recovery (immunes), no further centers of infection would exist so that the presence of the yellow-fever mosquito would no longer be a menace unless new human cases were brought in from other centers of infection. Also the mosquito transmitter (*Aedes aegypti*) was looked upon as an urban mosquito, not common or abundant in rural areas. Whether this conclusion can be accepted as fully proved is doubtful. That this mosquito does not occur far from human habitation appears well authenticated, and there seems no reason to doubt that it could become established about every human abode where it can survive. Given these conditions and the presence of monkey reservoirs, it would seem that the possibility of permanent yellow-fever centers is assured. Though an excellent vaccine is now available and most effective, it would be an entirely justified procedure for all cities, villages, towns, and other centers of population seriously to plan a strict control over this mosquito. If not, an outbreak of yellow fever involves almost a military supervision (as in the outbreaks in New Orleans, Rio de Janeiro, etc.). As this mosquito breeds practically only in artificial water containers, the consistent and continued elimination of these breeding places would result in such a permanent reduction of the numbers of this mosquito that the introduction of a few yellow-fever cases would not result in an outbreak of the disease. Though the disease has not reached the populous centers of northern, eastern, or southern Africa and India, yet the possibilities of modern transportation are constant sources of danger. Unless reduction of the yellow-fever mosquito is brought about, the appearance of the disease in any of these populous regions might mean a disaster of serious proportions, despite the use of the vaccine (as witness the outbreak in 1940 in the Anglo-Egyptian Sudan). Furthermore, new endemic centers would be established and the continued spread of the disease would be assured. In recent years (1933) the discovery of jungle yellow fever in South America has added a new problem to yellow-fever control. This should emphasize more strongly the need for urban control of *Aedes aegypti* and the more extensive use of the vaccine in suspected areas.

Though dengue is a disease of low mortality, yet the lowered vitality of its victims and the rapidity of its spread warrant special consideration. As *Aedes aegypti* is the only known transmitter in America, we must assume that it breeds in vast numbers in many southern states, as witness some 500,000 to 600,000 cases of dengue in Texas in 1922. The control of the mosquito is apparently not very effective in the United States. Here again the elimination of the breeding places of the yellow-fever mosquito should be a major consideration in every city and village where it occurs.

Malaria, unlike yellow fever and dengue, is primarily a disease of rural districts, small cities, and villages. The anopheline transmitters do not breed to any extent in artificial water containers but are primarily restricted to more or less permanent bodies of protected fresh water, slow-running streams, marshes, swamps, and, with certain species, to brackish water along coastal areas. Fortunately all anophelines are not "good" or "dangerous" transmitters of malaria. In recent years consistent efforts have been made to determine these "dangerous" transmitters, discover their specific breeding grounds, their bionomics, etc., and then concentrate all efforts, at first, to the control of such species. The results of such directed endeavors have been very gratifying in certain countries as the Federated Malay States, the Canal Zone, Palestine, etc. Whether such principles can always be applied remains for the future to decide. The reduction and control of anopheline vectors of malaria are highly specialized procedures. Such work should be guided by well-trained malariologists and entomologists, and the procedure to be followed must be based on a sound knowledge of the bionomics of anopheline vectors in any particular region (witness the problem of *A. gambiae* in Brazil).

PLAN OF ORGANIZATION

In order to plan and carry out mosquito control, a well-organized unit is essential. Such an organized division should be in close association with or directly under the officer in charge of public health work. This work may be done under local regulations or, where several communities unite, under a specific state or provincial law[3] empowering townships, districts, or counties to organize mosquito abatement districts. In any such organized district the work of mosquito control should be under a responsible, well-trained entomologist, or one familiar with the problems of mosquito biology. The success or failure will largely depend on his ability and freedom to plan and carry out effective measures. The budget for the proposed work should be independent and appropriated specifically for mosquito-control work. The officer in charge should be granted wide discretionary powers, and he should have authority to carry out well-planned schemes that may involve either private or public rights.

Such an officer should have authority to secure the co-operation of all public and private planning commissions, and all private or public bodies engaged in any operations that involve or may involve the formation of ponds, reservoirs, or impounded water, or that deal with building, street, road, and real estate developments, drainage schemes, etc. Only in this way will the officer have an opportunity to inspect all plans that might compel him to modify his scheme of mosquito control. The organized unit should include trained inspectors and laborers. The numbers and their equipment will be dependent on the extent of the abatement district and the difficulties involved. Furthermore, the officer should have authority to engage sanitary engineers and other experts when highly technical plans have to be prepared and carried out. In this way, one person will be held responsible and his success or failure can easily be judged by the mosquito density in his district.

Another important duty will be to aid the health authorities, public works departments, etc., in drawing up careful sanitary, drainage, and water storage regulations involving all conditions that may increase or decrease mosquito breeding. The expense of such an organization will depend on many factors. There is one consideration, however, that should outweigh the cost: any work done should be well done, a long-time plan of operations should be obtained, and a continuing policy should be assured. Furthermore, the cost of the improvements to public and private property may largely be charged to such properties and the general increase in taxable values should far exceed the costs.

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[3] Such laws are in effect in New Jersey, California, Illinois, and probably many other places. The New Jersey law seems the most far-reaching and adequate in our country.

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[4] The literature on mosquito control is very great. Fortunately several extensive accounts have recently been published and most of these contain bibliographies. Only a few references can be included here and the reader is referred to them for further information.

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CHAPTER XIII

Other Bloodsucking Nemocerous Flies: Simuliidae and Ceratopogonidae or Heleidae

IN ADDITION to the mosquitoes (Culicidae) and the moth flies (Psychodidae) two other families of Nemocera contain bloodsucking species. These flies are all very small, some of them extremely minute, but many of them are vicious biters and extremely annoying to man and animals. Recently certain species have been proved or incriminated as transmitters of important diseases. As these flies are world-wide in distribution, often extremely abundant in individuals, attack man and animals with terrible severity, and are now known to transmit certain diseases, the study of them has attracted considerable attention in recent years. Owing to their minute size and the difficulties involved in the study of their life histories, not as much progress has been attained as could be desired.

FAMILY SIMULIIDAE

The Black Flies, the Buffalo Gnats

The Simuliidae may be recognized by their small size (1 to 6 millimeters in length), stout bodies, short legs, and characteristic "humped" appearance due to an arching of the thorax (Fig. 145). The wings (Fig. 145) are broad with the anterior veins well developed, the others indistinct. The antennae are nine, ten, or eleven jointed and usually not as long as the head; the segments are short, closely pressed together, and bear numerous short hairs. In the males the eyes are contiguous (holoptic), while in the females the eyes are rather widely separated (dichoptic). The mouth parts are formed for piercing and sucking. Only the females are known to take blood.

The family includes at present a rather large number of species. Williston (1908) reported only about 75 species in all the world, but Bequaert (1931) records some 330 species, distributed as follows: 125 for the Palearctic region, 53 for the Nearctic, 80 for the Neotropical, 24 for the Ethiopian, 26 for the Oriental, and 24 for the Australasian. Dyar and Shannon (1927) report 47 species for North America and Greenland, and Bequaert (1926) indicates 70 species for South and Central Americas. Smart (1945) lists 623 world

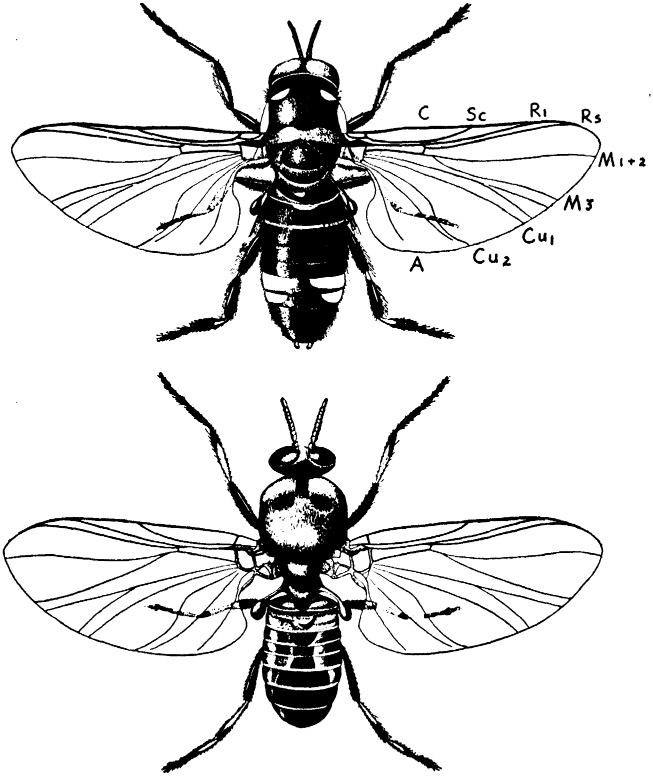
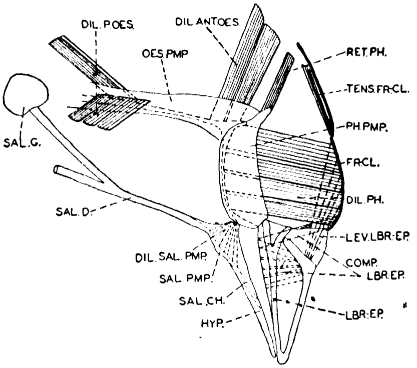


Fig. 145. The black fly, *Simulium arcticum* Malloch. Male above, female below. Veins are labeled according to the Comstock system. (From Cameron.)

species; Vargus (1946) adds 23 species to this list. The family is world-wide in distribution, extending from the tropics to the Arctic Circle and to elevations of at least 9000 feet.

STRUCTURE OF THE MOUTH PARTS: The mouth parts constitute a short proboscis composed of the following parts: The labrum. This is an elongated unpaired structure (in cross section like a three-sided pyramid) movably attached to the membrane suspended from the frontoclypeus. It is continued directly forward from the head as a strong convex plate strengthened medially and laterally by sclerotized bars that meet at the distal extremity. The base of each labral bar is more or less Y-shaped, the arms of the Y forming the bases of the lateral walls. These arms meet extensions from the head and the lower anterior walls of the pharyngeal pump. These points of contact form the fulcra for the levation and depression of the labrum. The arrangement of these parts and their muscles are shown in Fig. 146. The tip



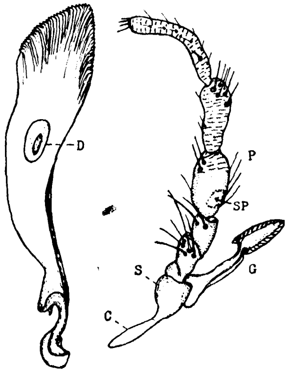


Fig. 146 (*left*). Lateral view of the mouth parts of a black fly (*Eusimulium lascivum*) to show the relationship of the various parts and their muscles. Comp lbr-ep, compressor muscles of the labrum; Dil ant oes, dilator muscle of the anterior esophageal pump; Dil ph, dilator muscle of the pharyngeal pump; Dil p oes, dilator muscle of the posterior esophageal pump; Dil sal pmp, dilator muscle of salivary pump; Fr cl, frontoclypeus; Hyp, hypopharynx; Lbr-ep, labrum; Lev lbr ep, levator muscle of labrum; Oes pmp, esophageal pump; Ph pmp, pharyngeal pump; Ret ph, retractor of the pharyngeal pump; Sal ch, salivary channel; Sal d, salivary duct; Sal g, salivary gland; Sal pmp, salivary pump; Tens fr cl, tensor of the frontal clypeus. (After Krafchick.)

Fig. 147 (*right*). Mouth parts of *Prosimulium hirtipes*. *Left:* Mandible. *Right:* Left maxilla, dorsal view. C, cardo; D, depression in mandible with elevation on opposite side; G, galea; P, palpus; S, stipes; SP, sensory organ. (Maxilla drawn at twice the scale of mandible.)

of the labrum is provided with denticles on each side of the median line. The mandibles (Fig. 147) consist of a pair of broad spatulate structures, sharply pointed distally and provided with numerous small recurved teeth along the apical margin. Each mandible has, near its middle, a small area with a depression on one side and an elevation opposite. In the position of rest the mandibles are closed scissorlike and lie between the labrum and hypopharynx. They are locked together by means of the device just mentioned, the elevation on one fitting into the depression of the other as first observed by Jobling (1928) for *Culicoides.* The maxillae (Fig. 147) are paired structures, arising just below the mandibles. Each maxilla has the usual parts: cardo, stipes (these two usually united), galea, and palpus. The galea has a curved, basal, sclerotized arm, which terminates in a vicious-looking, swordlike cutting structure (Fig. 147). The margins of the blade are recurved ventrally and bear retrorse teeth. The palpus consists of four segments (the basal one subdivided); the second segment has a deep pit in which is probably located a sensory organ. The hypopharynx is an unpaired organ lying below, and in close union at the base with, the labrum. It arises from the floor of the pharynx, with which it is joined by a hingelike arrangement. It is deeply concave on its dorsal side and its sclerotized margins receive, in V-like notches, the extensions of the lateral bars of the labrum. The salivary pump is attached near the base of the hypopharynx, and the salivary duct perforates the base of the hypopharynx and extends along its middle to near the apex. Back of the pharynx lies the pharyngeal pump. The labium consists of two lobes, each of which is concave anteriorly so that the mouth parts are concealed within when at rest. Each lobe is composed of three segments. The proximal parts are fused along the posterior mid-line while the other segments are free. The fused basal segments probably represent the theca and the free segments the labellae.

The action of the mouth parts in obtaining blood has not been observed or carefully described. In all probability they function as in *Culicoides* as described by Jobling (1928). He says, in describing their action,

> It was noted that the labrum-epipharynx, the hypopharynx, and the mandibles interposed between these two parts, compose together a piercing stylet which performs forward and backward movements during biting. When these mouthparts have penetrated a little more than half their length into the skin, the protraction and retraction cease. During the sucking of blood the mandibles are not withdrawn to the sides, but by the structure of their middle parts they are maintained between the labrum-epipharynx and hypopharynx. Thus the food canal is formed by them and the labrum-epipharynx as has already been indicated by Leon (1924).

The labium functions as a guide, holding the mouth parts in position while making the puncture. The action of the maxillae could not be observed by Jobling, but he thinks the galea moves forward and backward, thus having a tearing action.

BIOLOGY: The larval stage of all known species is passed in running water. The larvae are found in swift currents, at the edge of waterfalls, on rocks where the water sweeps by (Fig. 148), in shallow mountain streams, in roadside ditches, and in similar situations. They attach themselves by means of an anal disc (see below) and retain their position even in very swift water. They are usually found in the shallower parts of the streams, especially where the water breaks over some obstruction, or attached to floating grasses or other pendulous plants.

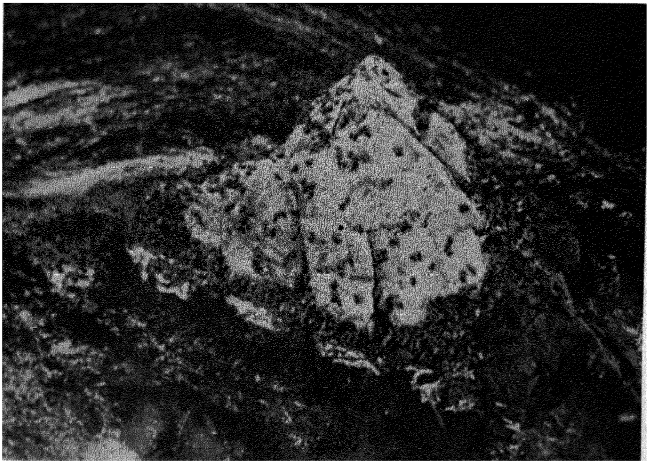


Fig. 148. Note the large stone sticking above the swift-running water. Near the water's edge and on the rock are large numbers of males of *Eusimulium muttatum* waiting for the emergence of the females. Below are large masses of larvae and pupae of this species.

The eggs are laid at the level of the water, or just below, on any convenient surface as bare rocks, debris, or other smooth objects (*Simulium pictipes*); on blades of grass trailing at the surface of the water (*S. vittatum, S. venustum, S. bracteatum*); or under the water to a depth of a few inches to a foot. Bradley (1935) states that *Cnephia pecuarum* drops its eggs directly in the flowing water; the eggs are heavier than the water and they settle to the bottom. The total number of eggs a single female may lay is not known, though Pomeroy (1916) records 349 eggs laid by one female, under experimental conditions, in twelve minutes. Other records indicate a female may lay as many as 500 or more eggs at one oviposition. According to most observations, oviposition takes place during the evening hours—from four to about eight o'clock. The eggs are minute, about 0.25 mm. in length and somewhat triangular in shape. They hatch in from 4 to 12 days or more, depending largely on temperature and aquatic conditions, or they may remain dormant for a long time.

The larvae (Fig. 149) of the Simuliidae can usually be recognized from their habitats. The more common, easily observed characters are the form of the body—generally subcylindrical, usually enlarged at each end, and attenuated in the middle; the possession of two large fan-shaped organs on the head; a short median leg armed with hooks on the ventral surface of the segment back of the head; a disc provided with rows of hooks arranged in circles on the posterior end of the body; and the presence of characteristic anal gills (blood gills). The larval stages of comparatively few species have been fully described. Edwards (1920) has summarized his work on the British species; Pomeroy (1916) has carefully described five American species; Friedericks (1920) many of the more common species of Germany; Puri (1932–1933) the Indian species; Gibbins (1933–1937) and Bequaert (1938) certain African species; Bequaert, Hoffman, and Vargas a number of species from Central America and Mexico; and Twinn (1936) many Canadian species.

The larva, on escaping from the egg, attaches to the nearest object by means of the thoracic proleg. The body is then moved about till the sucker-like anal disc can be brought into contact and more or less permanent attachment follows. According to Wu (1931), the anal disc is not a true sucker but attachment is brought about by glutinous material placed on the disc by the mouth. The larvae are capable of movement, looping from place to place by means of the proleg and anal disc. According to Puri (1925), this is accomplished as follows: the larva places some saliva on a selected spot and fixes the proleg to this spot; it then places saliva in front of the previous spot and, withdrawing the anal disc, attaches it to the new saliva. In this manner the larva can move slowly about. It also spins a silken thread from the salivary glands and can use this as a means of dropping down stream and then crawl back on the thread to the place of attachment.

The larva undergoes six molts, pupation occurring at the last molt. The duration of the larval period varies widely. Puri records four to six weeks (*S. aureum* and *S. erythrocephalum*) during the summer; Pomeroy notes full larval development in South Carolina in 17 days (*S. venustum, S. bracteatum, S. vittatum,* and *S. pictipes*); Cameron (1922) states that *S. arcticum* (*simile*) requires three to four weeks in western Canada; Wu (1931) records 13 to 17 days for *S. vittatum* in Michigan.

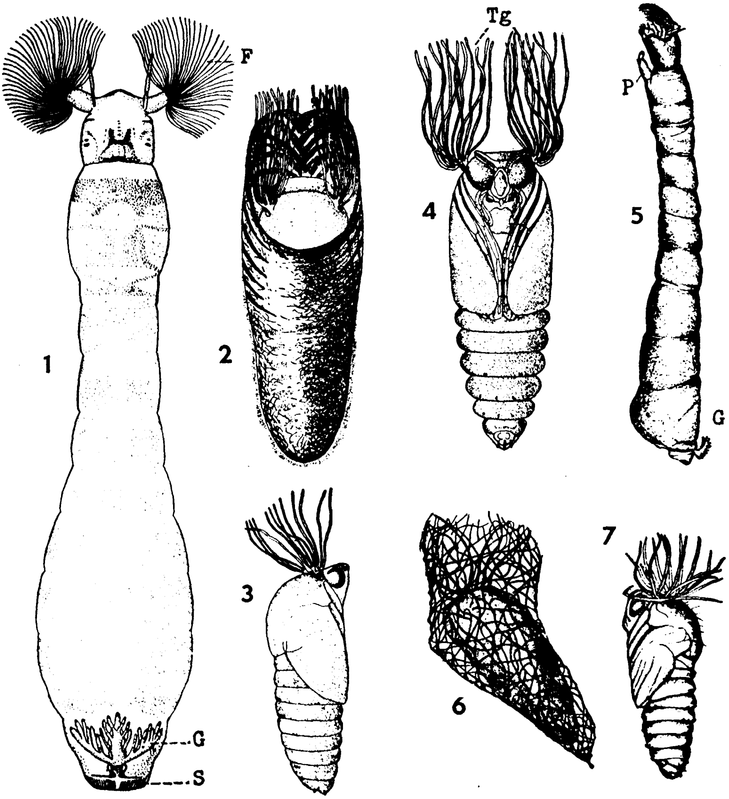


Fig. 149. (*1*) Dorsal view of larva of ***Simulium arcticum.*** (2) Pupa in its pupal case. (*3*) Pupa removed from pupal case. (*4*) Pupa, ventral view. (*5*) Lateral view of larva of *Simulium pictipes.* (6) Pupa in its case, lateral view. (*7*) Lateral view of pupa. F, mouth fans; G, blood gills; P, median prothoracic leg; S, posterior sucker; Tg, tracheal gills. (*1* to *4* from Cameron; *5* to *7* from Johannsen.)

Pupation takes place in the larval habitat. The larva spins a silken cocoon

(Fig. 149) within which the pupal period is passed. The pupal stage varies from two to seven days, or longer in cooler weather. The adults, on emergence, rise to the surface of the water and take to wing.

The number of annual generations varies greatly in different parts of the world. Pomeroy thinks that there are five or six generations in South Carolina; Cameron records four generations for *S. arcticum* (*simile*); Edwards thinks there is but one generation of *S. venustum* and *S. reptans,* two generations of *S. latipes,* three of *S. equinum* and *S. ornatum,* and four generations of *S. argyreatum* in England. Smart (1934) states there are four or five annual generations of *S. pictipes* in central New York; *Prosimulium magnum* has only one generation in the same area; *P. hirtipes* has frequently two generations in the Adirondack region of New York state and this is also true for *Simulium venustum;* Twinn (1936) records two or three generations of *S. vittatum* Zett. in Ontario and Quebec. Bradley (1935) records only a single generation a year for *Cnephia pecuarum.*

The adults are vigorous fliers and have been recorded four or more miles from their breeding grounds. Cameron (1922) records a 12-mile flight for *S. arcticum.* It is believed that their migratory habits are induced by their desire for blood, blood being the principal food of the adults (females). Most, if not all, the species are bloodsucking in habit (*S. aureum* is not known to take blood; *S. pictipes* is also thought to be an exception but it has been recorded as feeding on mules). Certain species seem to prefer the blood of particular animals though other species are more catholic in their tastes. Thus Pomeroy states that *S. venustum* seldom attacks man or cattle but is a severe pest of horses and mules, feeding within the ears. Dyar and Shannon (1927) report the same species as very annoying to man, and this agrees with the writer's experience. Bequaert (1938) summarizes the data on the feeding habits of black flies. Some feed largely on birds as *S. bracteatum* Coq. (= *aureum* Fries), *S. venustum* Say (important pest of ducks), *S. atratum* de Meij. (on birds in Java), *S. virgatum* Coq., and *S. mexicanum* Bellardi (on horses but not man in Guatemala); only 5 of the 57 species of the Ethiopian region attack man (*S. damnosum* Theo., *S. naevei* Roub., *S. adersi* Pom., *S. willmani* Roub., and *S. griseicole* Beck.). In addition we may add *S. venustum* Say and *S. hirtipes* Fries as severe pests of man in their ranges. Twinn (1936) reports *S. vittatum* Zett. as feeding on horses; *S. arcticum* Mal. is a severe pest of cattle, horses, and sheep; and in Mexico *S. metallicum* Bellardi, *S. ochraceum* Walk. and *S. callidum* D. & S. are known to bite man. Other species are known to be very destructive to animals including man, as *Cnephia pecuarum* (Riley) and *S. columbaschensis* Fabr.

CLASSIFICATION: The family Simuliidae has been rudely treated by the taxonomists. It has been divided into six or more subfamilies with numerous genera and subgenera (Enderlein, 1921). Edwards (1931), however, recognized but a single genus, *Simulium,* and seven subgenera. Vargas (1945) recognized but one genus, *Simulium,* for the New World species. Smart (1945) recognized two subfamilies and six genera from the world. Vargas (1946) adopts the classification by Smart but in addition adopts nine subgenera in the genus *Simulium* (restricted). The following key (adapted from Smart) will serve to separate the genera:

1. R_1 of the radius joining the costa about the middle of the front margin of the wing; radial sector (Rs) forked. (1 sp., California) .... *Parasimulium*

   R_1 of the radius joining the costa well beyond the middle of the front wing (Fig. 145); radial sector forked or not 2

2. Radial sector (Rs) forked; pedisulcus and calcipala lacking. (28 spp.) .... *Prosimulium*

   Radial sector (Rs) not forked (Fig. 145); pedisulcus and calcipala (Fig. 150) may be present or absent 3

3. Vein Cu_2 straight; anal vein straight; pedisulcus absent; calcipala well developed. (Neotropical; 13 spp.) .... *Gigantodax*

   Vein Cu_2 sinuous (Fig. 145); anal vein sinuous 4

4. Antennae with 10 segments or less (mainly Australian and Andean region of S. America) .... *Austrosimulium*

   Antennae with 11 segments; rarely 10 5

5. Pedisulcus absent or very indistinct; calcipala minute or absent; basal section of radius lacks macrotrochia above; distal section of radial sector with a single row of macrotrichia above. (World-wide; 36 spp.) .... *Cnephia*

   Pedisulcus present; calcipala present (Fig. 150); basal section of radius and distal section of radial sector with or without macrotrichia. (Worldwide; over 500 spp.) .... *Simulium*

It is not feasible to give keys to species as many characters are based on the male or female genitalia. Keys will be found in some of the references cited and these are indicated.

RELATION TO DISEASE

The black flies or buffalo gnats affect man and animals in at least two ways, by their bites and as intermediate hosts of parasites.

BITES: The bites of black flies are extremely annoying. The flies commonly appear in swarms and attack with great avidity. Various species have been recorded from the tropics to the polar circles as inflicting severe damage to stock and causing a peculiar fever in man. Probably the most famous species is the Golubatz fly (*S. columbaschensis* Fabr.), which frequently occurs in countless numbers in parts of Romania, Yugoslavia, and Hungary. Ciurea and Dinuflescu (1924) paint a gloomy picture of an invasion of this fly in certain parts of Romania during the season of 1923. Domestic animals suffered severely and the authors record the death of 16,474; large numbers of wild animals, as foxes, deer, and hares, were also killed. Though man was also severely attacked and suffered from their bites, no deaths are on record. Riley (1887) gives an extended account of outbreaks of *Cnephia pecuarum,* the buffalo or turkey gnat, in the lower Mississippi Valley. Mules, horses, cattle, sheep, sitting turkeys and hens, hogs, dogs, and cats suffered in the order named. Large numbers of these animals were killed, especially mules, horses, turkeys, hens, and hogs. Cattle also succumbed if weakened from poor food and exposure. There also appear reports of deaths of human beings but most of them seem doubtful. Webster (1904) gives a striking account of the plagues of this fly in the same region. Bradley (1935) reports heavy losses of mules in Mississippi and eastern Arkansas in 1927, 1931, and 1934. A total of over 1600 were killed during these years. Rempel and Arnason (1947) describe the mass attack of *Simulium arcticum* Mal. on horses, cattle, and sheep. The animals began dying within 6 to 24 hours after the attack. If cold weather intervened, the flies disappeared, and this happened in some of the worst outbreaks. In all, over 800 cattle, horses, and sheep were killed during the years 1944, 1945, and 1946. Various travelers and explorers give weird accounts of the abundance of black flies and the suffering caused by their bites. Wilhelmi (1920) presents an excellent summary of black-fly plagues (*die Kriebelmückenplage*).

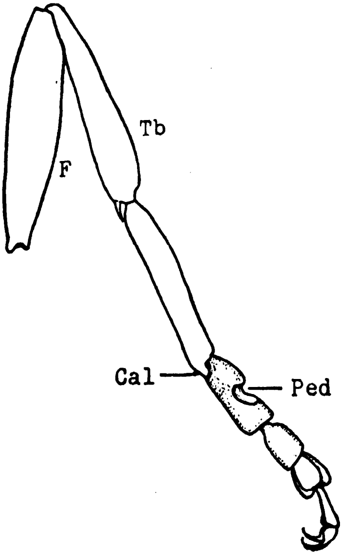
Stokes (1914) carefully investigated the effects of the bites of *Simulium venustum.* The typical bite in a susceptible individual appears to run the following course: bite painless, followed by hemorrhagic spots or red patches; a papular lesion develops in 3 to 24 hours, and later a vesicular lesion which may last for a few days to several weeks. The lesions from several nearby bites may become confluent presenting a large vesicopapular lesion with considerable exudate followed by extensive edema, and the formation of oozing and crusted plaques. Pruritus (intense itching) begins shortly after the bites and may become diffuse with considerable heat and burning sensation; the pruritus may return periodically even after the lesions have apparently healed. Frequently the intense itching, followed by scratching, may cause secondary infection with more serious results. As the flies frequently attack back of the ears, over the eyes, cheeks, and neck, inflammation and edema at these sites may be marked. In addition to the lesions, pruritus, etc., produced by the bites, most people suffer from swelling of the lymphatic glands (lymphangitis), which become tender and painful on pressure. These swellings usually subside without further trouble if the patient is not subjected to further black-fly attacks. Stokes records no constitutional effects from the bites though such have been noted by other workers.

There appears to be considerable immunity to the bites of black flies. Many persons reared in black-fly areas seem to acquire a certain immunity. The writer has suffered agonies from their bites, while native companions remained unattractive to the flies and unbitten. I have seen fishermen come from the woods with their faces streaming with blood due to black-fly bites but they suffered no apparent harm; others show distinct feverishness, irritation, and intestinal disturbances; in one case a lineman was brought in almost unconscious from continued exposure but he recovered in a few days.

The presence of these flies renders many attractive areas almost unhabitable during certain seasons of the year. Though attempts have been made to immunize man against their bites, no great success has been achieved. The activating agent in the causation of the vesicular papules, pruritus, etc., is believed to be in the secretions of the salivary glands but what it is remains as yet unknown.

DISEASE: Though black flies have been accused of transmitting diseases, it is only within the past few years that definite experimental work has proved them to be intermediate hosts of human parasites.

Onchocerciasis is an infection due to species of *Onchocerca* (family Filariidae of the Nemathelminthes). *Onchocerca volvulus* Leuck. causes subcutaneous tumors that vary from small, smooth nodules to swellings as large as a walnut (Fig. 151). In many cases no nodular swellings may occur, though the microfilariae can be recovered from the skin, the subcutaneous lymph channels, and the peripheral blood. This parasite was first found in a native of the Gold Coast, Africa, in 1893. Since then it has been found widely distributed along the west coast of Africa and from Sierra Leone to the Congo basin, east to southern Sudan, Uganda, Nyasaland, Kenya, and other parts of Africa. Blacklock (1926) reports that 40 to 50 per cent of the natives examined in Sierra Leone had the microfilariae of *O. volvulus* in their skins. In the same year he elucidated the further development of this worm in its insect vector. He discovered that a black fly, *Eusimulium damnosum* Theo., ingests these microfilariae; the ingested microfilariae show great activity in the gut of the fly and on the second day after feeding they are found in the posterior thoracic muscles; here development proceeds and molting apparently occurs. At the end of a minimum of six or seven days mature larvae are found in the labium of the proboscis and are ready to infect new hosts when the fly bites. Only man has been found naturally infected with



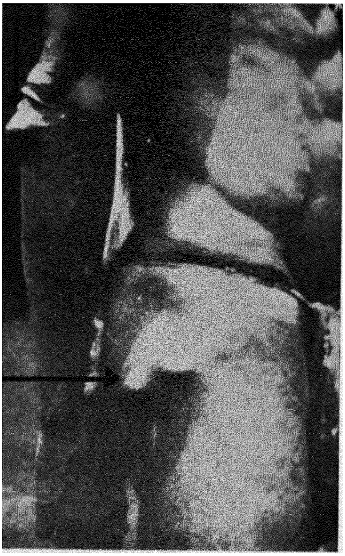


Fig. 150 (*left*). Hind leg of *Simulium vittatum*. Cal, calcipala; F, femur; Ped, pedisulcus; Tb, tibia.

Fig. 151 (*right*). Onchocerciasis. Note nodules on elbow and hip. (After Blacklock, *Annals of Tropical Medicine and Parasitology*.)

O. volvulus. Though no transmission experiments by means of experimentally infected flies have been attempted on man, it is believed that *Simulium damnosum* is the vector. Experiments with monkeys were negative. Though *S. damnosum* is widely distributed in tropical Africa, its early stages and breeding habits are apparently unknown.

Onchocerca caecutiens Brumpt was first found by Robles in 1915 in nodules on the scalp of about 95 per cent of the population of the Pacific slope of Guatemala at elevations between 600 and 2000 meters. The infection, in a certain proportion of cases, shows no clinical symptoms, but many have painful erysipelaslike swellings; hence it is called "coastal erysipelas." Recent workers seem to consider *O. caecutiens* identical with *O. volvulus.* Hoffman (1930) reports that all the people in certain parts of Chiapas, Mexico, have the microfilariae in the lymph and 86 per cent show nodular swellings. The nodular swellings occur, not only on the head, but on the iliac crests, ribs, shoulder blades, and other parts of the body. Ochoterena (1930) demonstrated the microfilariae in the excised eye of a blind man, the "embryos congregating in the outer third, in the corneal epithelium." Strong (1931) confirmed these results and states that the continued passage of these microfilariae through the lymphatics of the eye for long periods may cause conjunctivitis, keratitis, and iritis. It would thus seem that this parasite in Africa, Central America, and Mexico may be the causative agent of certain types of blindness.

Hoffman (1930) first traced the development of this microfilaria in a black fly, *Simulium callidum* D. & S. (= *mooseri*). He showed that the microfilariae, after being ingested by the black fly, pass from the intestine to the thoracic muscles where further development takes place. The developmental period in the fly is six or more days, and the infective stage passes to the mouth parts where the microfilariae are ready to infect new individuals when the fly bites. Hoffman, Strong, *et al.* and others have amply demonstrated complete development of this parasite in the following black flies in Mexico: *Simulium metallicum* Bellardi (= *avidum* Hoffman), *S. ochraceum* Walk., and *S. callidum* D. & S. (= *mooseri* Dampf).

In addition to the human diseases transmitted by black flies, O'Roke has shown that *Simulium venustum* Say transmits a malarialike disease of ducks caused by a protozoan, *Leucocytozoon anatis* Wickware. This disease is said to be very deadly to young ducklings. Johnson (1942) reports a *Leucocytozoon* of turkeys transmitted by *S. nigroparvum* Twinn. Steward (1937) has demonstrated the life cycle of *Onchocerca gutterosa* Neum. (a parasite of cattle) in the black fly, *Simulium ornatum* Meig. in England.

PROTECTION FROM BITES: Though certain persons claim immunity to black-fly bites, the effect on the average person is usually severe, even causing clinical symptoms of disease. Recently the United States Bureau of Entomology and other agencies during World War II have developed excellent repellents for mosquitoes, and some of these are effective against black flies. These are dimethyl phthalate and indalone. Everready or 612, developed at Rutgers University, is also an excellent repellent. Dimethyl phthalate and 612 are effective for about a maximum of four to six hours. Apply these repellents to all exposed parts but avoid getting them into the eyes; they may also be applied to stockings or other clothing through which the flies may bite. These repellents are pleasant, noninjurious to the skin, and can be applied as often as necessary.

CONTROL OF BLACK FLIES: The control of black flies is very difficult. As their breeding grounds are mainly swift or slow-flowing streams of all sizes, it does not seem possible to destroy the larvae except by the use of chemicals that may kill nearly all animal and plant life. The amount of such chemicals needed would be very great in some rivers where these flies often breed in vast numbers. In the smaller streams, however, breeding can be reduced by the removal of debris, such as logs, branches, stumps, stones, floating weeds or grasses, or other obstructions. The cost is usually excessive. Attempts have been made to reduce breeding by the application of DDT either as an oil emulsion or water suspension. The results are not very encouraging as the amount of DDT required kills so much of the other valuable animal life. It may be possible to devise methods and ascertain amounts that are effective against black-fly larvae but not injurious to other life in the streams.[1]

The adults, when abundant, may be killed by DDT as aerosols, mist sprays, etc., applied by airplanes, helicopters, or special ground equipment. Such methods have been applied extensively against hordes of mosquitoes and have proved satisfactory to those who pay for the expenditures.

FAMILY CERATOPOGONIDAE (Heleidae)

The Punkies, No-see-ums

The Ceratopogonidae contains a small number of known species, usually referred to as "punkies." This family may be distinguished by the long antenna (13 to 15 segments); the short proboscis (Fig. 154); and the membrane of the wings which bears micro- and macrotrichia and is commonly ornamented, in some genera, with dark spots and pale areas (Fig. 153). The family contains a considerable number of genera but only about four have species that are bloodsucking in habit. These are *Leptoconops, Lasiohelea, Holoconops,* and *Culicoides.* The most important genus is undoubtedly *Culicoides.*

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[1] Recent reports indicate that black-fly larvae can be destroyed, even in large streams, by airplane spraying some distance above their breeding grounds. How effective these measures are and the correct amounts of DDT to use have not been adequately determined. The destruction of other aquatic life in these streams is a problem that has not been solved satisfactorily.

KEY TO THE GENERA[2]

(Adults bite man or animals)

1. Radiomedial cross vein absent; antennae of females with 13 to 14 segments (including pedicel and minute scape) 2
   Radiomedial cross vein present; media with two branches; antennae of females with 15 segments (including pedicel and minute scape) 3
2. Antenna of female with 14 segments .... *Leptoconops*
   Antenna of female with 13 segments .... *Holoconops*
3. Empodium well developed, nearly as long as the claws. First radial cell small and narrow; second cell long and narrow. (Severe bloodsuckers; S. American) .... *Lasiohelea*
   Empodium small or vestigial; claws small and simple; two radial cells usually present and second branch of radius ends beyond middle of wing; wings usually spotted. (A large genus) .... *Culicoides*

THE GENUS *CULICOIDES*

The flies belonging to this genus are all bloodsucking and are usually known as "punkies." (The term "sand flies" is frequently used but this should be restricted to the bloodsucking species of Psychodidae.) They are extremely annoying and on account of their small size (only 1 to nearly 3 mm. in length) can easily pass through the openings of the ordinary mosquito screens. In some parts of the tropics and subtropics they are so abundant as to interfere seriously with the development of certain regions. Their mouth parts (Fig. 152) are admirably adapted for taking blood and closely resemble, in structure, the mouth parts of the Simuliidae. The males are not known to take blood.

LIFE HISTORY: Oviposition has apparently been observed in only one species, *C. kiefferi* Patton. This species lays its eggs in a mass in the vicinity of water, on some algae or green plant growth. Other species undoubtedly lay their eggs in a similar manner. The larvae are found only in water or in water-saturated sand or soil, both brackish and fresh, where there is decaying vegetation. They like water holes in stumps, tree holes, and manure heaps and water-holding plants; a few may be found in slime-covered bark of trees and under bark and rotting vegetation. The larvae (Fig. 154) are minute, elongate, cylindrical, nearly colorless, and difficult to find. The easiest method of obtaining the larvae is to collect water with the bottom debris and soil from suspected breeding places, place it in small jars, and allow the debris to settle. The larvae, if present, can then be seen performing their peculiar movements. They swim about eellike with a side-to-side movement of the anterior part of the body, followed, each time, by a similar motion of the posterior part. The length of the larval life does not seem to be known.

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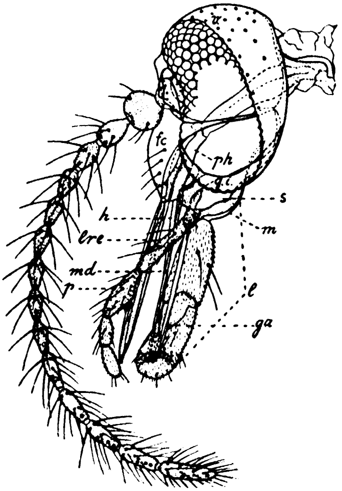
[2] The number of genera in this family varies widely depending on the author; Johannsen (1943) recognizes 45 genera in the Americas. Those indicated above are the only genera in which the species are bloodsucking in habit. For keys to genera and species, consult the bibliography.



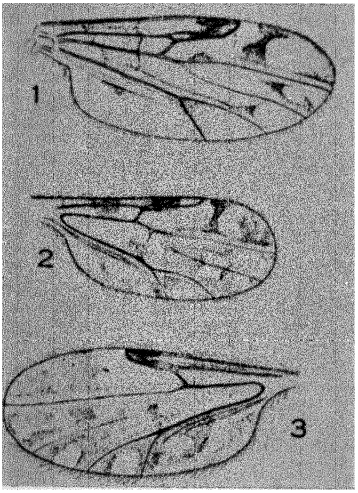


Fig. 152 (*left*). Head and mouth parts of *Culicoides pulicaris* L. fc, frontoclypeus; ga, galea; h, hypopharynx; l, labium; lre, labrum-epipharynx; m, mentum; md, mandible; p, palpus; ph, pharynx; s, stipes. (After Jobling, *Bulletin of Entomological Research.*)

Fig. 153 (*right*). Wings of *Culicoides* spp. (*1*) *C. cockerelli* Coq. (*2*) *C. diabolicus* Hoff. (*3*) *C. stellifer* Coq. (After Hoffman, *American Journal of Hygiene.*)

Pupation takes place in the water, on the surface of wet mud, at the water edge, or among algae. The pupa is elongate with conspicuous breathing trumpets arising from the thorax (Fig. 154). The breeding habits and bionomics of this group are imperfectly known.

Culicoides canithorax, C. meleus, and *C. dovei* (Fig. 154) are serious pests in many places along the Atlantic seaboard. In the West *Leptoconops torrens* is an abundant species in the Sacramento and San Joaquin Valleys. *Culicoides guttipennis* and *C. obsoletus* (*sanguisuga* Coq.) are widely distributed in North America and are annoying pests. *C. furens* Poey is widely distributed along the southern, western, and northern shores of the Gulf of Mexico, southeastern Florida, the West Indies, Bahamas, and down the Atlantic coast to Brazil.

The habits of the various species of *Culicoides* are not well known. Root and Hoffman (1937) record 33 species from North America and the Mexican highlands. They give very little information regarding their habits or bionomics. Johannsen (1943) lists 52 species from North America, Mexico, and the West Indies.

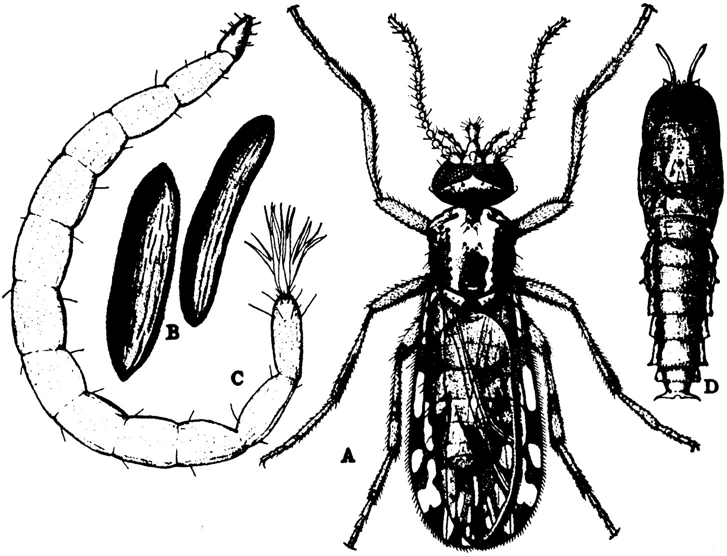


Fig. 154. Life stages of the salt-marsh punkie, *Culicoides dovei.* (*A*) Adult. (*B*) Two of the eggs. (*C*) Full-grown larva. (*D*) Pupa. (All enlarged; after Dove and Hall.)

OTHER GENERA

The species of *Leptoconops* and *Lasiohelea* are less well known. The adults, so far as observed, are known to suck blood and are said to be very annoying.

DISEASE

The punkies affect man and animals by their bites and by acting as intermediate hosts of parasitic worms. To most people the bite is very annoying. It is usually accompanied by a prickling sensation; later a reddened area appears about the point of puncture, which usually swells, and is followed by an intolerable itching that may last for days. No serious effects follow if scratching is avoided.

FILARIASIS: Sharp (1928), in the Cameroons, demonstrated that *Culicoides austeni* serves as the intermediate host of *Acanthocheilonema perstans.* This filarial worm is widely distributed throughout tropical Africa and coastal parts of South America from Venezuela to Argentina. It is not known to cause any specific human disease. The microfilariae are found in the peripheral blood of man, gorilla, and chimpanzee. These are obtained when the fly takes blood. Within the gut of *Culicoides austeni* the microfilariae are very active penetrating the gut wall within a few hours (six). About 24 hours later they are found in the thoracic muscles, where development proceeds. Six days later they migrate to the head and neck, and within a day or so more they are ready to emerge by way of the fly's proboscis. Though no actual passage of the larvae from the fly's proboscis through the human skin was observed by Sharp, it is believed that this species serves as an actual transmitter of this worm. *Culicoides grahami* has also been incriminated as a transmitter. Furthermore, in a dissection of 227 specimens of *C. austeni* caught in the wild, 7 per cent were found infected with the larvae of *A. perstans.*

Buckley (1934) demonstrated the developmental cycle of *Mansonella ozzardi* (Manson) in *Culicoides furens* Poey. This filarial worm of man occurs in parts of South and Central America, Mexico, and certain parts of the West Indies.

CONTROL OF SAND FLIES

No successful methods have yet been devised for satisfactorily controlling these pests. Hull *et al.* (1939) attempted control of breeding in marshes and mangrove swamps by diking and pumping the areas dry. When successful, good control was obtained. The application of insecticides has not been effective. The use of DDT in breeding areas might prove valuable. The treatment of screens, doors, and other woodwork about homes with a 5 per cent DDT in kerosene or other solvent has given some success in preventing these minute flies from entering homes. The use of repellents for personal protection is valuable. (See pp. 395-396.)

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CHAPTER XIV

The Tabanidae and Rhagionidae: Horseflies, Deer Flies, Clegs, Green-headed Flies; Snipe Flies

THE family Tabanidae is a very large one. Between two thousand and twenty-five hundred species have been described from the world; over three hundred species are recorded from North America. The adults are of stout build (Fig. 155); bristles practically absent; eyes large and prominent (contiguous in nearly all the males) and usually brilliantly colored (the colors disappear after death); antenna with the third joint annulated (Fig. 51 5) but never with a style; proboscis well developed, short (*Tabanus, Haematopota*), rather long

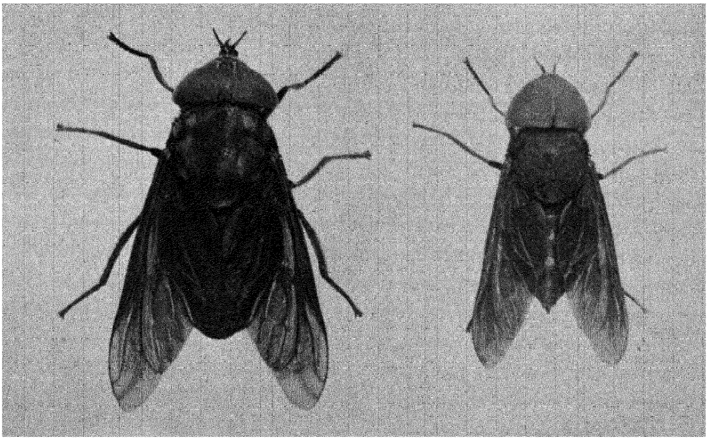

*Fig. 155. **Tabanus atratus*** Fabr. Female at left; male at right.

(*Chrysops*), or very long (certain *Pangonia* spp.); mouth parts adapted for piercing (Fig. 156); venation (Fig. 56) rather characteristic, the costal vein extending all around the wing. The squamae are large and the pulvilli and empodia are padlike.

In general the adults are robust, rather compact-looking flies; the powerful wings, stout depressed abdomens, and large, rounded heads give them the appearance of vigor and activity. They range in size from about that of the housefly (some *Chrysops* species) to the large *Tabanus* species with a wing expanse of over two and one-half inches. The females of the great majority of the species are bloodsucking in habit, while the males peacefully take only plant juices, nectar, excreta of some other insects, or any available liquids containing nutritive material. The females have a wide range of hosts, the larger mammals, especially our domestic animals, being most frequently attacked. Certain species are known to attack crocodiles and others obtain blood from sea turtles, biting between the plates on the back. In many parts of the world they are serious pests of livestock, and cattlemen frequently suffer serious losses from outbreaks of these flies. Webb and Wells (1924) state that a medium-sized tabanid requires 8 to 10 minutes to feed and takes about 0.125 cubic centimeters of blood; Stone (1930) estimates that such a fly takes nearly 0.2 cubic centimeters for a meal. It will thus be seen that when these flies are very abundant the daily loss of blood must be a serious drain.

The flies are lovers of sunlight, warmth, and moisture. They are attracted to moving objects, and species of *Tabanus* and *Chrysops* consistently attack man. During dark, cloudy days, or cool, rainy weather they remain inactive, resting quietly in secluded places. Their range of flight must be considerable, though no one has apparently investigated this phase of their activities. MacCreary (1940) reports the collection of adults at light traps located 3 to 8 miles offshore. They are much more abundant near their breeding grounds—swamps, marshes, irrigated land, river bottoms, along the margins of rivers and lakes, and in similar places—than in the open, drier country. The length of the adult life is apparently not very long, probably not over four weeks to two months as shown by Stone (1930) from his consistent weekly collecting data. In Louisiana Jones and Bradley (1916 and 1917) present somewhat similar data, which indicate a longer season for the activity of the adults of certain species (*Tabanus vicarius, T. lineola, Chrysops flavidus*). In the region of central New York and no doubt elsewhere (as indicated by Jones and Bradley in Louisiana), the emergence and flight activity of the different species take place at rather definite periods of the year. As a result, the maximum abundance of any one species may be concentrated in a rather short period (as

Tabanus pumilus in midsummer) or somewhat prolonged in the case of those species that normally emerge later in the season.

THE MOUTH PARTS OF A HORSEFLY (*Chrysops* sp.): In the horsefly the mouth parts project downward and look like a cylindrical sac with a pair of palpi overlapping it (Fig. 156). The saclike appearance is due to the enlargement of the labium, which is hollowed out on its anterior face and terminates in two lobes, the labella. Within this hollow lie the mouth parts for piercing. These consist of a long dagger-shaped labrum, a pair of saber-shaped mandibles, a pair of bladelike maxillae with their palpi, and a long

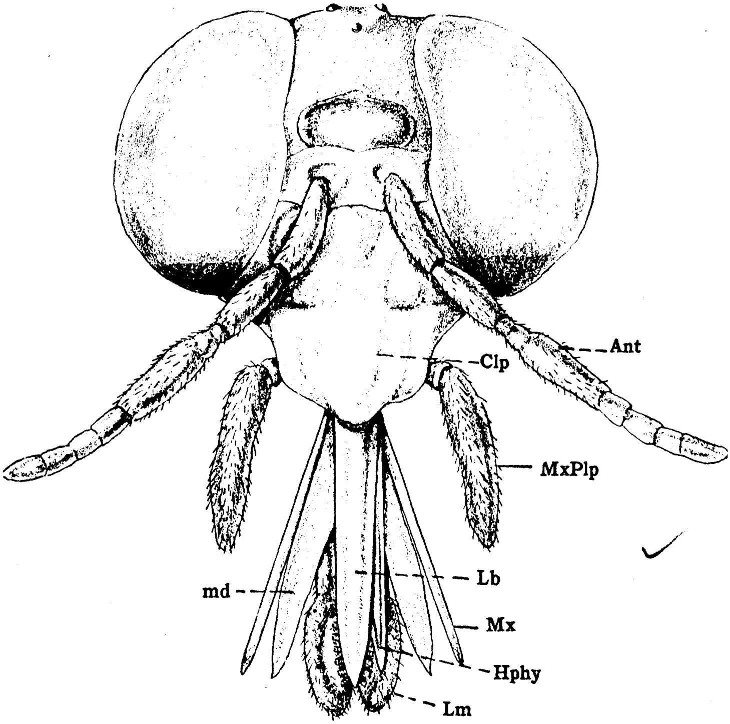

Fig. 156. Frontal view of the head and mouth parts of a horsefly (*Chrysops univittatus*). The mouth parts are withdrawn from the labium in order to show them separately. Ant, antenna; Clp, clypeus; Hphy, hypopharynx; Lb, labrum; Lm, labium (the dotted line points to the tip, usually called the labella); md, mandible; Mx, maxilla; MxPlp, maxillary palpus.

tapering stylet, the hypopharynx. The details of these structures and their muscles are shown and explained in Fig. 157. The labium is a large, thick organ, deeply grooved along its anterior face, and terminates in the two broad lobes called the "labella." In the normal position the labella are closed, but they can be spread apart like broad, soft pads. The posterior portions of the labella are firmly united, but the anterior halves are separated by a deep median cleft. The undersurface of each lobe is traversed by close-set channels called "pseudotracheae."

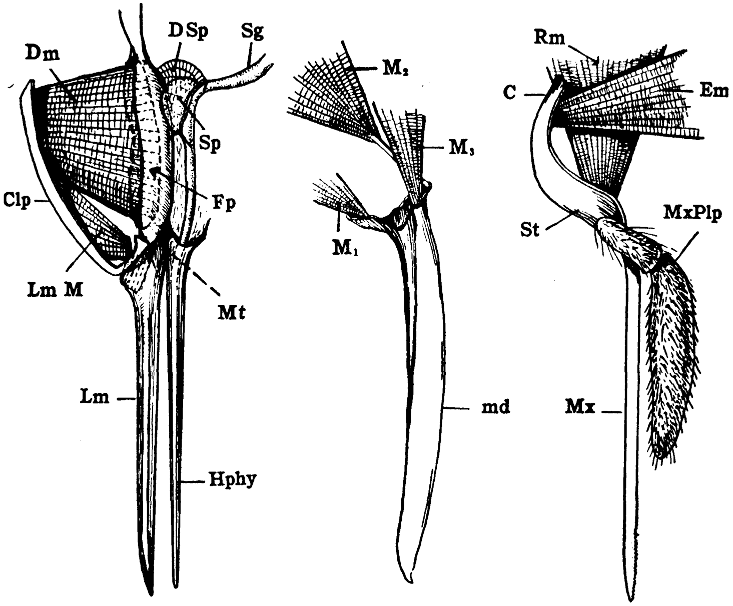

Fig. 157. Mouth parts of a horsefly (*Chrysops univittatus*). *Left:* Labrum and hypopharynx showing their relationship and their connection to the head and some of the muscles (the hypopharynx is slightly withdrawn in order to show it more clearly). *Center:* The right mandible with muscles in place. *Right:* The left maxilla with its muscles. C, cardo; Clp, clypeus; Dm, dilator muscle of the food pump; DSp, dilator muscle of the salivary syringe; Em, extensor muscle of the maxilla; Fp, food pump or pharyngeal pump; Hphy, hypopharynx; Lm, labrum; LmM, labral muscle; M_1, M_2, M_3, muscles that move the mandible; md, mandible; Mt. mouth; Mx, maxilla; MxPlp, maxillary palpus; Rm, retractor muscle of maxilla; Sg, common salivary duct leading to salivary syringe (note the two valves, one at entrance to syringe and one at exit); Sp, salivary syringe; St, stipes.

The action of these mouth parts is difficult to determine. The probable action is as follows: the fly spreads its soft, padlike labella on the skin, drives the mandibles into the skin, and by means of the powerful mandibular muscles rips it. By continuing such action the mouth parts, except the labium, are driven deeper and deeper into the flesh. The barbed ends of the maxillae probably act as holdfasts, and the mandibles by muscular action can be twisted in the wound. By this means blood soon flows rapidly and is pumped by the food pump up the channel made by the labrum and hypopharynx. The salivary secretion is forced into the wound by the salivary pump. This secretion is said to possess an anticoagulin and an irritant to facilitate and increase blood flow.

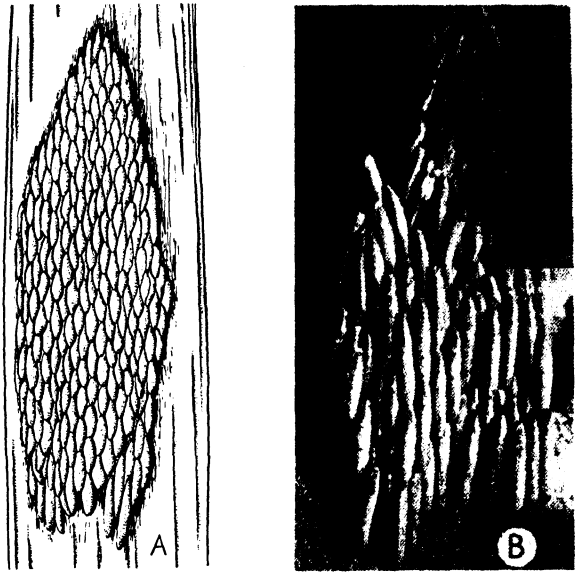

Fig. 158. Egg masses of horseflies. (*A*) Egg mass of *Chrysops* sp. (*B*) Egg mass of *Tabanus phaenops*. (*B* after Doten.)

LIFE HISTORY: As the larval life of practically all our common species is passed in water, wet soil, or semiaquatic conditions, the eggs are laid in the vicinity of such situations. The places of oviposition may be classified as follows (according to Stone, 1930):

1. Foliage or other objects over shallow, quiet water, edge of shallow pools, lakes.

2. Foliage or other objects in relatively deep water at some distance from shore, or on ledges, or rocks, over deep water.

3. Stones or other objects projecting over flowing streams.

4. Vegetation, as leaves or trunks of trees, over either moist or even quite dry soil.

The eggs are deposited in masses (Fig. 158), varying in number from 100 to 800 eggs. The species of *Chrysops* usually place their eggs in a single layer (Fig. 158 *A*), though *C. celer* and *C. pikei* place theirs in double tiers; those of *Tabanus* are generally laid in several layers (Fig. 158 *B*). The egg masses are protected by a gluey, waterproof covering, placed on them by the female when in the act of oviposition. The egg stage, normally, lasts but a short time, usually not more than 5 to 7 days, though it may be prolonged by cool, unfavorable weather. All of the eggs of a mass hatch at about the same time, and the larvae immediately drop to the water or the ground beneath.

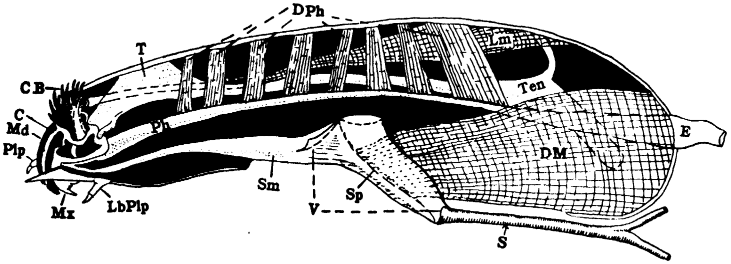

Fig. 159. A sagittal sectional view of the head of a tabanid larva to show the relation of the mouth parts to the pharynx. C, canal through the mandible; CB, cephalic brush of spines; DM, dilator muscle of the salivary pump; DPh, dilator muscles of the pumping pharynx; E, esophagus; Lm, levator muscle of the mandible and maxilla and the cephalic brush; LbPlp, labial palpus; Md, mandible; Mx, maxilla; Ph, pharynx; Plp, maxillary palpus; S, common salivary duct; Sm, salivary duct from pump to labium; Sp, salivary syringe; T, anterior extension of the tentorium; Ten, tentorium; V, valves of the salivary pump. (Redrawn and modified from Cameron.)

The larvae are primarily carnivorous and cannibalistic; some species are undoubtedly saprophagous (many *Chrysops* spp.). The larval mouth parts are adapted for piercing and extracting the contents of their victims (Fig. 159). The length of the larval life varies considerably. In most of our North American species the larval stage requires from 9 to 11 months though, undoubtedly, the amount and availability of food determines, to a large extent, the time of pupation. Under laboratory conditions Webb and Wells reared *Tabanus punctifer* from the egg to the adult stage in less than two years. The rearing conditions were abnormal and, in nature, the larval growth is completed probably in less than a year. Stone (1930), Schwardt (1936), Logothetis (unpublished thesis), and others have reared considerable numbers of Tabanidae. The average larval life of those reared was about 11 to a little over 12 months, while the pupal period varied from five days to two or three weeks. However, certain larvae of the species required nearly two years (as *Tabanus vicarius* in its northern range).

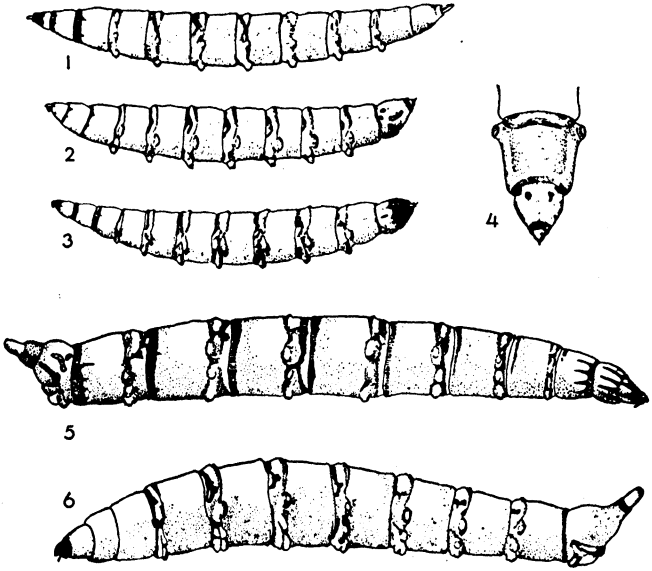

Fig. 160. Larvae of Tabanidae. (*1*) *Chrysops discalis* Will. (2) *C. excitans* Walk. (*3*) *C. fulvaster O.S.* (*4*) Siphon of *C. excitans.* (*5*) *Tabanus reinwardtii* Wied. (*6*) *T. septentrionalis* L. (From Cameron, *Bulletin of Entomological Research.*)

The larvae of Tabanidae possess 11 body segments exclusive of the small retractile head (Fig. 160). The body is cylindrical, tapering toward both ends, usually striated longitudinally, and with a single posterior siphon. The siphon is borne on the dorsal portion of the anal segment. It can be telescoped within the anal segment and bears on its tip the openings of the respiratory system (metapneustic). In addition, the presence of Graber's organ within the tenth and eleventh segments (readily seen in most tabanid larvae) will distinguish these larvae from all others. The organ consists of a series of capsules, each containing a pair of minute, black pyriform bodies, lying in a pyriform sac directly beneath the integument of the tenth and eleventh segments. In the case of *Goniops chrysocoma,* the larva has a club-shaped body, swollen posteriorly, and the striations are overshadowed by the mammillated parts of the integument; Graber's organ is not easily seen and no distinct siphon is visible.

When the larvae are mature they migrate to drier, rather compact soil where they pupate. The pupal period is rather short, ranging usually from one to three weeks.

CLASSIFICATION

The family Tabanidae contains a large number of genera, at least over sixty.[1] Surcouf (1921) presents a key to the genera of the world; Kröber and Bequaert give us a review of most of the African species; Hine (1903) treats of the North American species; and other workers give incomplete accounts of the species from different parts of the world. Bequaert (1924) states that in America, north of Panama, there are over 334 species distributed among 21 genera; of this number 71 belong to the genus *Chrysops* and 206 to the genus *Tabanus;* the other genera contain from 1 to 18 species. Brennan (1935) gives an excellent account of the subfamily Pangoniinae and Stone (1938) that of the subfamily Tabaninae for North America. Philip (1947) attempts a rather new classification of the Tabanidae, dividing the family into the normal subfamilies and these into tribes (3 tribes in the Pangoniinae; 4 tribes in the Tabaninae) and recognizes 27 genera with 474 species for North America north of Mexico. However, the following brief key will aid in placing the more common species in their correct genera. For the identification of the larvae, Stone (1930) gives preliminary keys to the immature stages of the North American species (*Chrysops, Tabanus,* and *Goniops* spp.) which he knew.

KEY TO SOME OF THE NORTH AMERICAN GENERA

1. Hind tibiae with spurs at the tips; ocelli usually present .... Subfamily *Pangoniinae* 2
   Hind tibiae without spurs at their tips; ocelli absent .... Subfamily *Tabaninae* 7
2. Third segment (the flagellum) of antenna with 5 distinct annuli 3
   Third segment of antenna with 8 distinct annuli 4
3. Pedicel (2nd segment) of antenna about one-half as long as the first segment (the scape) .... *Silvius*

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[1] Enderlein (1922, 1923) recognizes over 150 genera from the world, many of them with but one or two species.

Pedicel more than one-half as long as the scape, often nearly as long; wings usually infuscated, picturelike .... *Chrysops*

4. Eyes of females acutely angulate above; basal portion of wing infuscated .... *Goniops*

Eyes of female not angulate above; wings of uniform color 5

5. Maxillary palpi short, stubby, about equal in length to the proboscis .... *Apatolestes*

Maxillary palpi slender, shorter than proboscis 6

6. Cell R_5 petiolate .... *Esenbeckia*

Cell R_5 open, not petiolate .... *Stonemyia*

7. Third antennal segment with 4 annuli; wings gray, with small white spots .... *Haematopota*

Third antennal segment with 5 annuli; wing pattern, if any, not as above 8

8. Basal part of third antennal segment without a dorsal projecting tooth; eyes bare; wing with at least a subapical brown spot .... *Diachlorus*

Basal part of third antennal segment with or without a dorsal projecting angle; if angle is present eyes are bare (not pilose) 9

9. Eyes distinctly pilose; ocellar tubercle absent; eyes of female with a single diagonal, purple line (usually present even in dried specimens). Palpi not black and abdomen without a dorsal stripe .... *Atylotus*

Eyes pilose or bare but without the diagonal line; either the palpus black or the abdomen with a narrow, dorsal stripe .... *Tabanus* .... *Stenotabanus*

NOTES ON SOME OF THE GENERA: The genus *Tabanus* contains a vast assemblage of species, over a thousand being listed from the world; Bequaert (1924) reports over two hundred from North America north of Panama, while Stone (1938) recognizes 124 species in North America north of Mexico. Most of the species are large (Fig. 155), stout, vigorous fliers and readily attack man and animals.

Chrysops is the next largest genus, the species being world-wide in distribution; over eighty species are recorded from North America. They are commonly called "deer flies." The species are rather small (Fig. 161). The wings are clear except for a broad, dark area along the anterior margin of the wing and a broad, dark band across the wing at the level of the discal cell or just beyond it; the apex may be clear or infuscated. They readily attack man and are often extremely annoying. Most of the species are partial to low-lying marshy or swampy woods.

Silvius is a small genus of which we have six species in North America.

Representatives of this genus occur abundantly in the Australian region.

The species of the genus *Haematopota* are most abundant in the Ethiopian and Oriental regions, though they occur in all parts of the world. Only two species are recorded by Stone (1938) as occurring in North America.

In the genus *Pangonia* the eyes are more or less broadly separated in the female, whereas in the male they may be contiguous or separated. Ocelli are usually present though they may be absent. The proboscis is of variable length, but it is generally longer than the head and frequently very long. The sixth longitudinal vein is straight. This genus has been broken up into a number of genera of rather doubtful validity.

The genus *Diachlorus* is practically restricted to South America. One species, *D. ferrugatus* Fabr., is known from North America (Delaware to Florida and Mexico to Brazil).

RELATION TO DISEASE

In addition to the effects of their bites and the loss of blood, man and animals suffer from certain diseases that are distributed by tabanids either mechanically or as intermediate hosts.

FILARIASIS

Loa loa Cobbold is a filarial worm that has been recovered at various times from man for over a hundred years. The earliest observations (1770–1825) were on Negroes recently imported into the West Indies. Later this worm was found in its indigenous territory in West Africa. At present it is widespread along the west coast from Nigeria and the Cameroons down to Angola and inland to central tropical Africa and possibly to Uganda. The mature female worm measures from 50 to 70 mm. in length and about 0.5 mm. in maximum width; the male from 30 to 34 mm. in length to about 0.4 mm. in width. They are found in the subcutaneous tissues of man where they migrate back and forth. They have been found in various parts of the body but seem to have a predilection for the head, especially the eye (hence often called the "eye worm"). Frequently these worms appear to produce swellings, the so-called "Calabar swellings," which may become as large as half a goose egg. These swellings are generally painless, hot, and disappear in a few days. What relation the worm bears to the swellings has not, apparently, been determined.

The females discharge microfilariae in the passages made during their migrations. These reach the peripheral blood vessels, where they are found during certain parts of the day (9 A.M. to 2 P.M.), hence were called *Microfilaria diurna* by Manson. On epidemiological grounds Manson (1895) suggested that a species of mangrove fly (*Chrysops dimidiata* v. d. Wulp) was the intermediate host. Leiper (1912, 1913) and Kleine (1915) added certain experimental evidence in support of this view. However, the Connals (1921 and 1922) completely elucidated the entire life cycle of this worm. From dissections of wild specimens (2283) of *Chrysops dimidiata* and *C. silacea* they found 0.96 per cent infected with filariae. Experimentally they showed that these flies take up the microfilariae while feeding; the microfilariae then bore their way out of the gut and lodge in the thoracic and abdominal muscles; here further development takes place and in 10 to 12 days after the infective meal mature larvae appear in the proboscis. The fly is now ready to infect new hosts. Most of the larvae leave the fly at its first meal, though it may remain capable of infecting new hosts for at least five days. The Connals were able to infect, experimentally, guinea pigs, rabbits, and a monkey. The two tabanids, *C. dimidiata* and *C. silacea,* are strictly diurnal in their feeding habits and feed commonly on man. In all probability other species of bloodsucking flies will be found capable of transmitting this filarial worm.

TULAREMIA

Tularemia is an infectious disease caused by *Bacterium tularense* (*Pasteurella tularensis*). Primarily it occurs in nature as a plaguelike disease of rodents, especially rabbits and hares. It is transmitted to man by various bloodsucking insects (see Chapter III). It is of interest here because Francis (1919, 1920) first recognized the identity of "deer-fly fever" and the "plague-like disease of rodents." By careful experiments Francis and Mayne (1921) were able to demonstrate the agency of *Chrysops discalis* (Fig. 161) in disseminating the disease from infected to healthy guinea pigs and rabbits. They found the method of transmission was purely mechanical, though the fly could remain infective as long as 14 days. They found that practically all the flies did remain infective at least as long as eight days after their infecting meals. They also demonstrated that numerous human cases of tularemia were due to the bite of this fly, the fly obtaining the bacterium from jack rabbits and transmitting it to man. Cases due to the bite of *Chrysops discalis* have been reported from Utah, Idaho, Wyoming, Colorado, Nevada, Oregon, and Montana.

ANIMAL DISEASES

The species of Tabanidae are extremely annoying and injurious to livestock and many of the larger game animals. Not only do these animals suffer from their bites and consequent loss of blood, but the flies frequently distribute pathogenic organisms from one animal to another. This is due to the fact that frequently the flies, not being allowed to complete their blood meal on one host, immediately attack another. In this way they may transmit, mechanically, any organism on the proboscis obtained from the previous host. The principal types of disease transmitted in this manner are those in which the virulent organisms are present, in large numbers, in the peripheral blood and somewhat resistant to short exposures to the air. Here are found such diseases as anthrax, trypanosomiasis, hemorrhagic septicemia, etc.

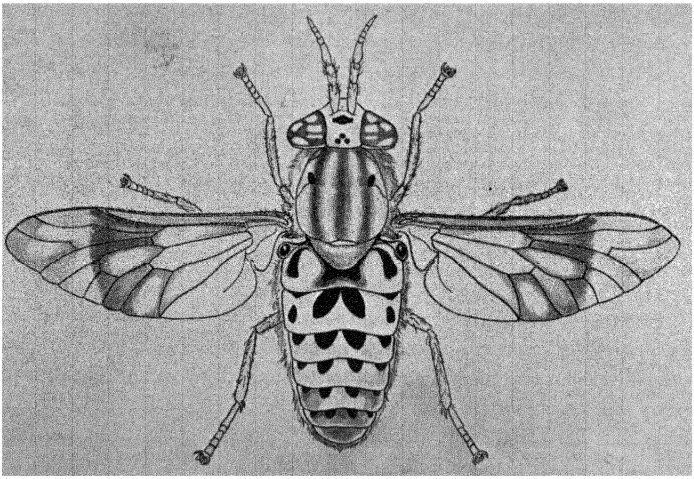

Fig. 161. Chrysops discalis Will. (After Francis.)

ANTHRAX: A few investigators have demonstrated the possibility of the mechanical transmission of this disease from animal to animal by biting flies, principally Tabanidae. Mitzmain (1914) proved in a number of controlled experiments that *Tabanus striatus* could transmit anthrax from infected to healthy animals. This was accomplished by the method of interrupted feeding, the fly feeding on a heavily infected guinea pig and then transferring within a short time to a healthy one. If flies were allowed to feed on infected guinea pigs a short time after their death and were then transferred to healthy pigs, no infection resulted. Though his experiments were few in number, he demonstrated the possibility of species of Tabanidae distributing the disease in nature. Morris (1918) obtained a high percentage of infection by feeding a *Tabanus* sp. on dying guinea pigs (from four hours before death till 20 minutes after death) and then immediately feeding them on healthy pigs. Herms states that physicians have told him of the infection of man (malignant pustule) by the bites of horseflies.

TRYPANOSOMIASIS: Various species of trypanosomes have been shown to be transmitted mechanically on the proboscis of different species of horseflies. It would be entirely possible for almost any bloodsucking tabanid to do this provided it could feed for a brief period on an infected animal and then be immediately transferred to a susceptible host. The trypanosomes are injected, provided they are present within or on the proboscis in a viable condition, into the new host at the time of biting. Some of the important trypanosomes that have been shown capable of being transmitted in this manner are *T. evansi* (causative agent of surra), principally by species of Tabanidae and also by *Stomoxys calcitrans* and *S. nigra* (as this trypanosome has no known intermediate host in which a cyclical development takes place, the only known method of transfer is by biting flies); *T. soudanense* (believed to be only a variety of *T. evansi*), which causes a chronic disease, eldebab, of camels and is transmitted by horseflies; and *T. hippicum,* which causes a trypanosomiasis of mules and horses in South America and parts of Central America and is transmitted by *Tabanus importunus* (Colombia and Venezuela). In Panama, Dunn (1932) and Clark and Dunn (1933) demonstrated that the vampire bat (*Desmodus rotundus murinus*) is the important vector. *T. annamense,* another horse-infecting trypanosome in Annam and Tonkin, is transmitted by tabanid species; *T. equiperdum,* the causative agent of dourine in horses, has been shown to be capable of transmission by bloodsucking flies, *Tabanus nemoralis* and *Stomoxys calcitrans* (this trypanosome is normally transmitted by direct contact of mucous surfaces as in coitus; it has no known intermediate host).

CONTROL

No successful methods of controlling horseflies have as yet been devised. The reduction of possible breeding areas by drainage is suggested, and Webb and Wells (1924) point out that no breeding took place in well-drained areas. Recently Logothetis and Schwardt (1948) found numerous larvae of *Tabanus vicarius* (*costalis*), one of our most abundant horseflies, in dry upland soil such as pasture land, cornfields, and cabbage fields. As many tabanids have the habit of flying over pools, dipping their bodies into the surface of the water, Portchinsky suggested the application of kerosene oil to the surface of pools favored by the flies. He tried several experiments with most gratifying results. The oil would have to be applied when the flies are abundant and at various periods to meet the time of emergence of the different species. Webb and Wells record an egg parasite, *Prophanurus emersoni* Girault, as an effective check on the breeding of *Tabanus punctifer.*

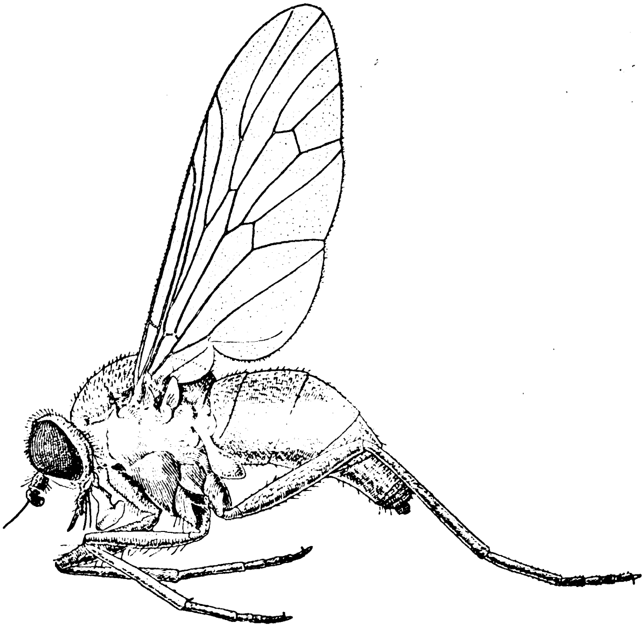

Fig. 162. Symphoromyia atripes. (After Ross, *Annals of the Entomological Society of America.*)

THE RHAGIONIDAE (LEPTIDAE)

The Snipe Flies

The Rhagionidae consists of rather small, or medium-sized, dark flies, found commonly in woodlands, especially near moist places. Unlike the horseflies, they are rather sluggish and easily captured. Both adults and larvae are predaceous. However only two genera are known to be bloodsucking in habit, *Symphoromyia* in North America and *Spaniopsis* in Australia. The species of *Symphoromyia* can be recognized by the kidney-shaped third antennal segment. About 25 species of *Symphoromyia* are known from North America and most of these species are from the mountainous regions of the West. Practically none of these have been taken in lowlands or valleys.

S. hirta Johnson is a large species (7.5 mm. in length) and is widely distributed in North America. Its flight habits resemble those of *Chrysops* spp. and its bite is rather severe. Mills (1943) describes an outbreak of this fly in the mountains of southwest Montana, the flies attacking viciously and being very troublesome to game animals. *S. atripes* Bigot (Fig. 162) is prevalent in parts of the mountains of western America and it is recorded as causing as much or more annoyance than mosquitoes. It attacks quietly and Ross (1940) records it as extremely annoying in the mountains (above 5000 ft.) in British Columbia. *S. pachyceras* Will. and *S. kincaidi* Ald. are also reported as bloodsucking in habit in parts of the Pacific coast area.

As far as known, the biology or breeding habits of none of our bloodsucking species are known. Other species of rhagionids are known to breed in moist soil where there is decaying vegetation

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CHAPTER XV

The Bloodsucking Muscoidean Flies: Muscidae, Subfamily Stomoxyidinae

THOUGH the great majority of flies belonging to the family Muscidae are nonbloodsucking in habit (see Chapter xvi), a small, closely related group, the Stomoxyidinae, are bloodsucking and are of great importance to the medical man and the veterinarian. These flies belong to the genera *Stomoxys, Haematobia* (*Siphona*), *Glossina, Stygeromyia, Haematobosca, Bdellolarynx,* and possibly a few others. The species of *Stomoxys* and *Haematobia* are widely distributed throughout the world; those of *Glossina* are restricted practically to the African continent; the other genera have representatives in the Oriental and Ethiopian regions. In the Americas we have practically only two species, *Stomoxys calcitrans* and *Haematobia irritans,* which are widely distributed and of considerable importance. None of these bloodsucking species except *Glossina* spp. and *Stomxys* spp. have, as yet, been incriminated as intermediate hosts of pathogenic organisms.

THE BITING STABLE FLY

Stomoxys calcitrans Linn.

The biting stable fly is a close relative of the housefly but can be distinguished by the sharp, piercing, nonretractile proboscis, the distinct rounded spots on the abdomen (Fig. 163), and the wing venation. This bloodsucking fly is widely distributed throughout the world and may be found wherever man and his domestic animals occur. It has been called the stable fly because of its common occurrence in and around stables, though it also frequents houses (particularly in late summer and autumn) and is often known as the "biting housefly" or "dogfly." It is a lover of the open and often occurs in immense swarms about cattle, especially throughout our central states from Texas to Canada and in the Argentine Republic. This fly is a vicious biter and attacks a great variety of animals as well as man. Bishopp (1931) reports that mules, horses, cattle, hogs, dogs, cats, sheep, and goats are subject to attack in about the order named. The loss of blood due to these flies when they are abundant is a serious drain, and in severe outbreaks many animals may die or be so weakened that other diseases develop and cause death. Furthermore, both Bishopp and Freeborn have recorded a marked reduction of milk flow and beef production when these flies are plentiful.

The bloodsucking habit of this species caused it early to be suspected and later incriminated as a mechanical distributor of numerous animal and human diseases. It has been shown to be the intermediate host of at least one nematode, *Habronema microstoma,* and a cestode, *Hymenolepis carioca.*

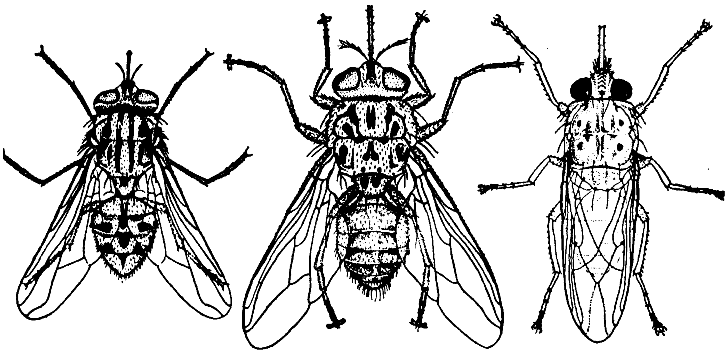


Fig. 163. Biting flies. *Left: Stomoxys calcitrans. Center: Glossina palpalis. Right: Glossina* fly in resting position.

The mouth parts (Figs. 164,168) are admirably adapted for piercing and taking blood. Unlike the mosquito, the stable fly uses the entire proboscis in making the wound and both males and females suck blood. The parts consist of those found in the housefly (see pp. 134–139), but greatly modified to meet the needs of piercing. The *rostrum* (Fig. 164 *a*) is much smaller and the pharyngeal skeleton or fulcrum is not so well developed or heavily sclerotized. Owing to the acute flexure of the proboscis between the rostrum and the haustellum, there is a marked difference in the structure of the buccal cavity. The prepharynx appears as a large cylindrical duct, and the outer wall is composed of thick rings forming a supporting framework for the food channel. *Haustellum:* The labium is strongly sclerotized, enlarged, and bulbous at the base tapering to the apex; it appears like a club. Its upper surface is grooved to form a deep labial gutter in which lie the labrum and hypopharynx. Both of these are shorter than the haustellum and do not reach the base of the labella, attaining only the labellar sclerites (furca). The food channel is formed by the juncture of the margins of the labrum and the hypopharynx and opens directly into the pharynx (Fig. 164). *Labella:* The labella are small, oval lobes, much reduced as compared with those of the housefly (Fig. 164 *b*). When at rest the lobes are closely appressed along their inner face, concealing completely the cutting and tearing apparatus. When the lobes are expanded two

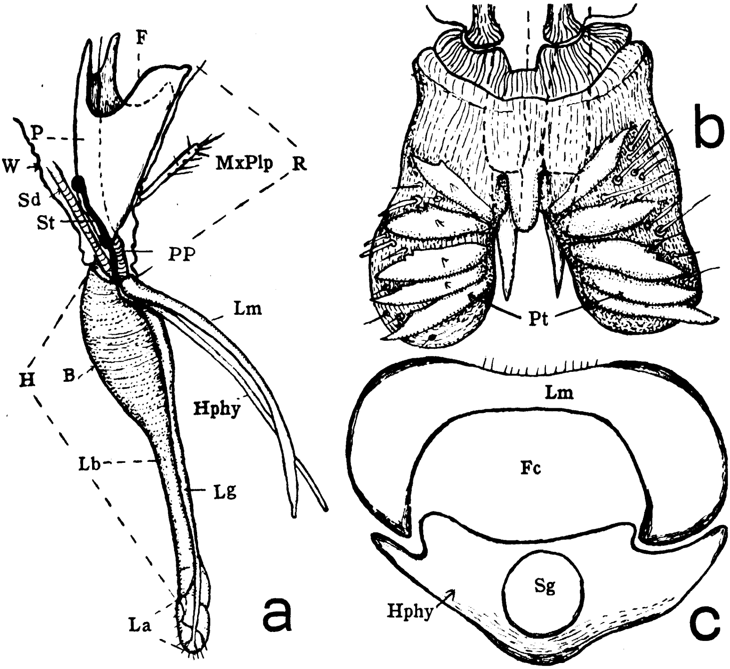
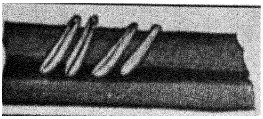


Fig. 164. Mouth parts of the stable fly (*Stomoxys calcitrans*). (*a*) Side view of the proboscis. (*b*) The labella of the proboscis with the prestomal teeth exposed. (*c*) Cross section of the labrum and hypopharynx near the middle of the proboscis. B, swollen base of the labium; F, fulcrum; Fc, food channel; H, haustellum; Hphy, hypopharynx; La, labellum; Lb, labium; Lg, labial gutter; Lm, labrum; MxPlp, maxillary palpus; P, pharynx; PP, prepharynx; Pt, prestomal teeth; R, rostrum; Sd, salivary duct; Sg, salivary duct in hypopharynx; St, stipes; W, chitinous membrane.

series of teeth are exposed, five on each side attached to the discal sclerite. Between the teeth may be observed a number of leaflike blades that aid in the tearing of tissues. The labellar sclerite is not so prominent as that of the housefly. In biting, the stable fly brings the rostrum and haustellum into line, the labella are everted, and by means of the labellar teeth and leaflike structures the skin is punctured. The labella are sunk into the wound so that the blood may be drawn up the food channel into the pharynx.

LIFE HISTORY

The most common breeding grounds are horse manure and straw stacks. It has been found breeding in cow, sheep, and other manures when mixed with considerable amounts of straw. Other common breeding grounds are the leftover grains and straw about dairies, piggeries, etc. It has also been found breeding in fermenting piles of grass, weeds, peanut wastes, and other vegetable rubbish. Intensive breeding is reported in fermenting seaweed piled up by the sea along the northern shores of parts of the Gulf of Mexico. Moisture is essential for the development of the larva. Wet, soggy manures, edges of rotting straw stacks, and fermenting grass piles are frequently found swarming with the larvae during warm, damp weather. This species has never been found breeding in human excrement.



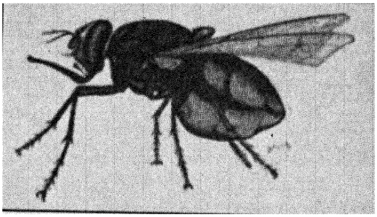


Fig. 165 (left). Eggs of *Stomoxys calcitrans* attached to straw. (After Bishopp.)
Fig. 166 (right). *Stomoxys calcitrans.* Female engorged with blood. (After Bishopp.)

The newly emerged female requires a number of blood meals (Bishopp thinks at least three) for the production of eggs. She lays her eggs in irregular masses, usually a few to as many as 25 in a single group (Fig. 165). A female may lay several batches (as many as 122 eggs) before seeking another blood meal. A single fly may lay eggs at least three times, taking several blood meals between ovipositions. Bishopp (1931) records a maximum production of 632 eggs by a single female.

The egg is elongate-ovoid, of a creamy-white color, and measures about 1 mm. in length. The incubation period varies from two to five days, usually three days (at a temperature of 70° F.). The young larvae immediately bury themselves in their food and development is quite rapid. With an abundance of food, moisture, and summer temperatures (75° to 85° F.) the larvae reach maturity in about two to three weeks; at higher temperatures maturity may be reached in 11 days but, in cool weather, larval development may require a month or more. The full-grown larva measures about 20 mm. in length, is white to creamy white in color, and resembles very closely the larva of the housefly. It may be distinguished, however, by the narrower, more pointed anterior end and by the posterior spiracles (Fig. 195 5). In the biting stable fly the posterior spiracles are widely separated, rather triangular in shape, and heavily sclerotized; in the housefly they are close together and nearly D-shaped.

Pupation takes place usually in the drier parts of the breeding grounds, either toward the margins or near the underlying soil. The chestnut-colored puparia measure from 5 to 7 mm. in length and may be distinguished by the posterior spiracles (the spiracles are those of the last larval instar, Fig. 195). The pupal period varies greatly and is dependent largely on temperature, varying from 6 to 20 or more days. The entire life cycle from the egg to adult may be completed in as few as 14 days, though the normal period is usually three to four weeks. Under unfavorable conditions the life cycle may be greatly prolonged—seven or more weeks.

HABITS OF THE ADULT

These flies are lovers of the open and commonly congregate on sunny walls, fences, and other exposed situations. During storms, dark days, and at nightfall they seek shelter, invading barns, houses, or any available shelter. On the open prairies they often occur in immense swarms and render life almost unendurable not only for cattle but also for man. However, their most common habitat is about stables and farmyards where a constant blood supply is available. Both the males and females are vicious bloodsuckers. The bite is painful, but once the beak is inserted and the flow of blood starts, little, if any, pain is felt. The fly requires from two to five minutes to obtain a full blood meal. When fully gorged (Fig. 166) it flies away rather sluggishly, settling on some nearby object to digest its meal. During warm weather digestion is very rapid and the flies require two meals a day. In cool weather they usually require a full day to digest a single blood meal.

They are vigorous fliers and will follow their food supply for considerable distances. How far they can travel does not seem to be known. However, considerable distances may be traversed along roadways, the flies taking a blood meal, settling down to digest it, and then following another passing host. In this way the adults may be found long distances from their breeding grounds. They have been observed in trains, automobiles, etc. The life of the adult is rather long, varying from a few days to as many as 72 days for the female and 94 for the male (Mitzmain). As a rule the probable length of adult life is not over three or four weeks.

In warm climates, breeding is continuous throughout the year. In the southern United States breeding is intermittent during the winter months and the larval life is greatly prolonged. In the colder parts of North America the winter months are passed normally in the larval and pupal stages.

RELATION TO DISEASE

Though the biting stable fly has been accused and, in some cases, apparently incriminated as a vector of pathogenic organisms, most of the recent work indicates that this fly plays but a small part in the spread of diseases.

POLIOMYELITIS: A very considerable amount of work has been done on the part it may play in the transmission of poliomyelitis; though at first incriminated all later researches tend to prove that it has no part in the spread of the disease. Furthermore, the advances made in the study of the disease point to the improbability that any bloodsucking insect could act as a vector. It would seem more probable that flies that prefer fecal wastes and nasal discharges would be incriminated as vectors. As a matter of fact, recent work has incriminated such flies (see p. 476).

TRYPANOSOMIASIS: This fly has been shown to act as a mechanical vector of a number of species of trypanosomes. *Trypanosoma evansi,* the causative agent of surra (see Chapter XIV) of horses and mules, is known to be distributed by it. This is especially true when flies are abundant and blood meals are interrupted, the fly passing directly from one animal to another. The trypanosomes are transported on the proboscis and can withstand at least ten minutes' exposure to the air. In some parts of the world species of *Stomoxys* are regarded as important agents in the spread of surra.

Under experimental conditions *Stomoxys calcitrans* has been shown capable of infecting susceptible animals with the following species of trypanosomes (there is no development or multiplication of the trypanosomes in the fly):

Trypanosoma brucei (causative agent of nagana)
Trypanosoma rhodesiense (causative agent of Rhodesian sleeping sickness)

Trypanosoma gambiense (causative agent of Gambian sleeping sickness)
Trypanosoma cazalboui, T. dimorphon, and some others

In order to bring about the transfer by the fly it must obtain the trypanosomes from an infected animal and then feed, usually within ten minutes, on a susceptible animal. Infection takes place through the living trypanosomes in or on the proboscis of the fly.

INFECTIOUS ANEMIA OF HORSES: A virus disease of horses, infectious anemia, is widespread in North America, Europe, and Japan, and probably other countries. In recent years this disease has been shown to be transmitted by the interrupted feedings of *Stomoxys calcitrans* from the sick to the well by Scott (1922) and by Stein *et al.* (1942). The latter authors have also demonstrated sufficient virus in the mouth parts of certain tabanids as well as *Stomoxys calcitrans* that have fed on sick animals to infect susceptible animals.

The genus *Stomoxys* contains a considerable number of species, probably twenty or more depending on the authority consulted. Zumpt (1938) lists some 27 species, all of which except the one described above occur in the African or Oriental regions. None of these appear to be of much medical importance.

CONTROL

The control of the biting stable fly consists essentially in the elimination or reduction of their breeding grounds. The treatment and handling of manure for the prevention of the breeding of the housefly (see Chapter XVI) is also effective against this species. Cleanliness in the handling of feeds in and around piggeries, stables, etc., will eliminate many breeding places. However, the most important breeding ground of this fly is in strawstacks, especially when they become wet and rotting and heating take place. In order to reduce breeding, strawstacks should be built with vertical sides and the top so arranged as to shed as much water as possible. The base of the stack should be cleaned up so that no rotting and heating straw accumulates. All straw not intended for the feeding of animals or other use should be spread over the fields and ploughed under or it should be piled and burned. Old strawstacks should not be allowed to stand, for they usually become centers for the breeding of enormous numbers of flies. Such stacks should be distributed over the land or burned. Intensive breeding also occurs in fermenting vegetable rubbish, such as stacked peanut wastes, fermenting seaweed piled along shore lines, and any fermenting plant wastes. The employment of DDT sprays gives excellent promise for the control of the adults. In using DDT follow the directions on the containers.

THE HORN FLY

The horn fly (*Haematobia irritans* Linn.) is rather small, only about one-half as large as the biting stable fly. It is primarily a pest of cattle and acquires its name from its habit of clustering at the base of the horns. It rarely, if ever, attacks man. The species breeds exclusively in fresh cow dung. Though the fly is a serious pest of cattle, it is not known to be of any great importance in the transmission of diseases. It is not of any medical importance.

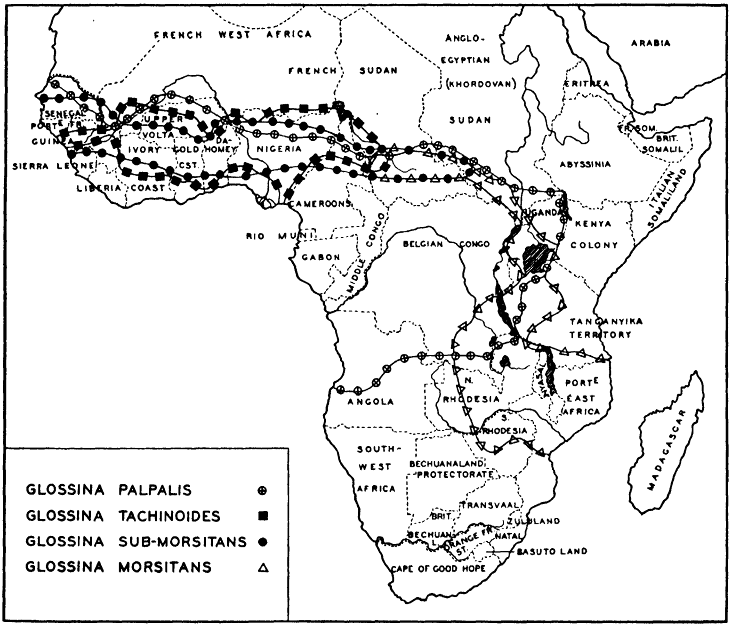

FRENCH WEST AFRICA
FRENCH SUDAN
ANGLO-EGYPTIAN SUDAN
(KHORDOVAN)
ARABIA
ERITREA
FR. SOM.
BRIT. SOMALIL.
ABYSSINIA
ITALIAN SOMALILAND
SENEGAL
PORT. GUI.
FR. GUI.
SIERRA LEONE
LIBERIA
IVORY COAST
UPPER VOLTA
GOLD CST.
DAHOMEY
NIGERIA
CAMEROONS
RIO MUNI
GABON
MIDDLE CONGO
BELGIAN CONGO
UGANDA
KENYA COLONY
TANGANYIKA TERRITORY
ANGOLA
N. RHODESIA
NYASA.
PORT. EAST AFRICA
S. RHODESIA
MADAGASCAR
SOUTH-WEST AFRICA
BECHUANALAND PROTECTORATE
TRANSVAAL
BRIT. BECHUANA L.
ORANGE FR. ST.
NATAL
ZULULAND
BASUTO LAND
CAPE OF GOOD HOPE
GLOSSINA PALPALIS ⊕
GLOSSINA TACHINOIDES ■
GLOSSINA SUB-MORSITANS ●
GLOSSINA MORSITANS △

Fig. 167. Distribution of the important *Glossina* flies in Africa. (Adapted from the latest map showing this distribution.)

✓THE *GLOSSINA* OR TSETSE FLIES

The *Glossina* or tsetse flies are primarily inhabitants of tropical and subtropical Africa, various species occupying different or overlapping areas of the continent. The only record of any species having been found outside Africa is from southeast Arabia and this record is doubtful. Their distribution in Africa lies between a line drawn from the mouth of the Senegal River east through Lake Chad to the Nile and thence to the coast at about 4° North latitude south to a line drawn from the mouth of the Cunene River east through the southern boundary of Angola to the northeastern extremity of St. Lucia Lake in Zululand (Austen). Within this area Newstead (1924) recognizes 20 species, 1 subspecies, and 5 varieties. The various species are not widely distributed throughout this vast region but occupy certain areas, some closely restricted to districts suitable for their development, as *G. swynnertoni* Austen, or widely distributed over a vast area, as *G. palpalis* and *G. morsitans* and their varieties (Fig. 167). This genus is probably one of the most important among insects. The flies are the transmitters of many species of trypanosomes, especially the important pathogenic species—those causing sleeping sickness of man and nagana of cattle, horses, and a wide variety of game animals.

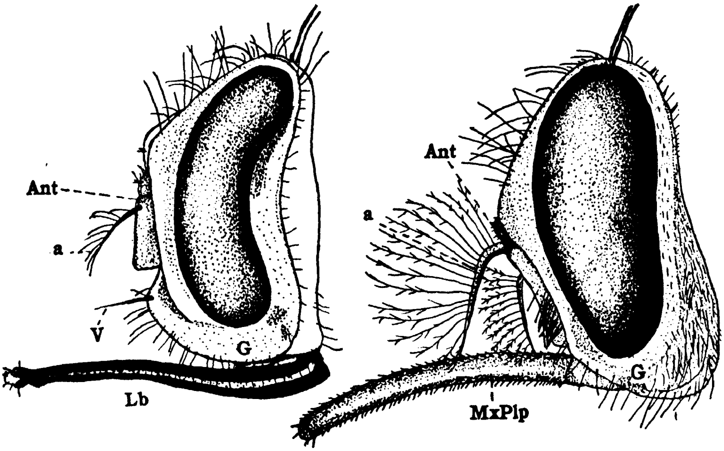


Fig. 168. Heads of bloodsucking flies. *Left: Stomoxys calcitrans. Right: Glossina* sp. a, arista (note the difference); Ant, antenna; G, the gena; Lb, labium; MxPlp, maxillary palpi (within these lie the labium and piercing mouth parts); V, vibrissa.

In structure these flies closely resemble *Stomoxys* but they differ rather markedly in certain features. Their life histories more nearly approach some of those of the Pupipara rather than those of the typical muscids. The more important external characteristics can be summarized here but very briefly. The adults, when at rest, hold their wings crossed scissorlike (see Fig. 163) over the abdomen. The wing venation is also quite distinctive. The proboscis is held in front of the head and appears large and stout owing to the development of the maxillary palpi. The palpi are thick, porrect structures. Each palpus has a broad, flat channel on its inner face. The proboscis lies within the channel formed by the apposition of the palpi (Fig. 168).

The proboscis consists of the rostrum, haustellum, and labella. The rostrum is very short, pyramidal in shape, and compact. Extending at right angles from its distal end lies the haustellum. The haustellum resembles that of *Stomoxys*. At its base is a large, bulbous structure usually known as the "bulb." The labium extends to the labella as an elongated sclerotized structure and grooved along its upper surface (the labial gutter). Within the labial gutter lie the labrum and hypopharynx. The labella are not well marked off from the labium proper. On the inner face of the labella are rasps, prestomal teeth, and certain accessory structures that serve to penetrate when the fly seeks blood. Both males and females are bloodsucking in habit.

BIOLOGY OF *GLOSSINA* SPECIES

Though the *Glossina* flies are distributed over an extensive area in Africa, they are not found everywhere but are restricted to particular tracts, known as "fly belts." These "belts" may be very limited owing to the conditions necessary for the species to obtain food, shelter, and an opportunity to reproduce. As the knowledge of these flies is far from complete, the biology of the two most important species is here briefly considered.

GLOSSINA PALPALIS ROBINEAU-DESVOIDY: This species (Fig. 163), the transmitter of Gambian sleeping sickness of man, is distributed throughout central Africa (Fig. 167), in an area bounded by a line drawn from the mouth of the Senegal River east to southern Ethiopia, thence south to the southern end of Lake Tanganyika, and west to central Angola (here reaching the Atlantic Ocean). Within this extensive area the fly occurs primarily along watercourses, rivers, and lakes bordered with forests having undergrowths. The flies do not wander far from water, generally not over a few hundred yards. Shade is essential, but it may vary from dense vegetation to more or less open forest or even the tall grass and sedges along rivers or lakes. The flies are most active during the hours of sunshine and are attracted to moving objects. They seem to prefer dark skins and clothes to light-colored skins or clothes. The preferred food of this species seems to be the blood of man, though they attack various domestic and game animals such as pigs, goats, monkeys, hippopotamuses, crocodiles, bushbucks, waterbucks, mongeese, etc. The adults are long lived, the average length of life varying from about 100 to over 250 days.

LIFE HISTORY: Unlike most of the muscoidean flies, the *Glossina* species do not lay eggs. Though the eggs are formed they pass singly into a uterine pouch where they hatch. Only a single egg is received by the uterine pouch at a time. Here the egg hatches and the larva completes its growth within this peculiar uterus. The food for growth is supplied by special glands, the so-called "milk glands." Roubaud found that the period of gestation of the first larva produced by a female was 22 days and the intervals between subsequent larvae varied from 9 to 10 days. The mature larvae are deposited in dry soil situated in close proximity to water and in the shade. The pupal period varies from 25 to 55 days.

GLOSSINA MORSITANS WESTWOOD AND *G. SUB-MORSITANS:* These species occupy extensive areas in central, western, and eastern Africa (Fig. 167). The "fly belts" of these species are not so restricted as of *G. palpalis.* They have a widespread distribution during the wet season. Shade and moisture do not appear so essential, for these flies may be found long distances from water. During the dry season they concentrate in certain areas where there is some shade, as among the nondeciduous trees or fresh green grass in the extensive, open, low-lying country. This green grass is supported by subsoil water and affords excellent grazing for game animals, which, in turn, furnish an abundant food supply for the flies. The flies travel considerable distances, especially when following animals. There seems no doubt that they can migrate from five to ten miles. Many observers state that the flies are most active during the cool of the day, morning and evening hours, though others record them as biting in the brightest sunshine in the heat of the day.

LIFE HISTORY (*G. morsitans*): Unlike *G. palpalis, G. morsitans* is not dependent on the proximity of water for its breeding grounds. The females deposit mature larvae in loose, dry soil; the pupae have also been found in hard soil, in wood ash from forest fires, and in other situations. Some kind of shade seems essential though this may be furnished by shrubbery, fallen trees, overhanging rocks, tree hollows, or burrows in the ground. In general the breeding grounds of this species appear to be widely scattered over its entire range. The pupal period varies from about 21 to 60 or more days, dependent largely on temperature.

RELATION TO DISEASE

The *Glossina* flies are the transmitters of various species of trypanosomes, the most important affecting man being *Trypanosoma gambiense* (the causative agent of Gambian sleeping sickness), *T. rhodesiense* (causative agent of

Rhodesian sleeping sickness and believed to be a variety of the following species), and *T. brucei* (causative agent of nagana or tsetse-fly disease of horses, dogs, cattle, and game animals). Trypanosomiasis is the general term applied to infection with any species of *Trypanosoma. Trypanosoma* species are Protozoa, belonging to the class Mastigophora, subclass Zoomastigina, family Trypanosomatidae. The trypanosomes are found as parasites in the blood stream, occasionally in the tissues, of vertebrates. A great number of species has been described, and many of them, if not all (with the exception of *T. equiperdum* and *T. evansi*) require an invertebrate host for the completion of their life cycle and transmission to new hosts. The body of a typical trypanosome (Fig. 169) appears as a curved, narrow leaf or flattened blade. The ends are tapering, one end usually being blunter than the other. The nucleus is generally central and the blepharoblast lies near the blunt or posterior end. From the kinetonucleus arises the flagellum, which passes out of the body and forms the outer border of the undulating membrane and may be continued as a free flagellum beyond the body. Reproduction is by binary fission.

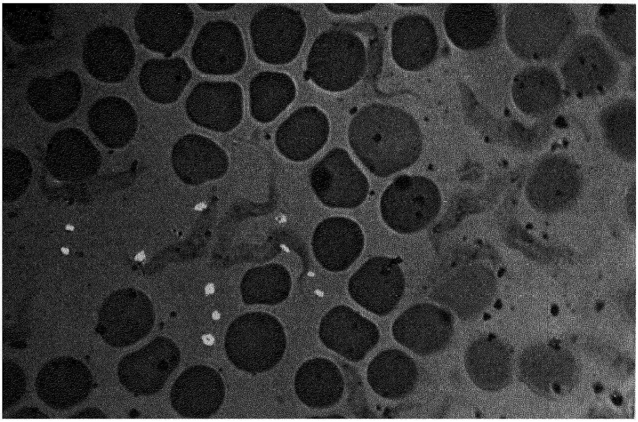


Fig. 169. Trypanosoma rhodesiense in blood of guinea pig.

Though there are numerous species of trypanosomes, only a comparatively few are known to be pathogenic. The species known to be pathogenic to man are *T. gambiense, T. rhodesiense* (Fig. 169), and *T. cruzi.* The first two are restricted to tropical Africa and are transmitted by *Glossina* flies; the last one occurs in South America and is transmitted by bugs of the family Reduviidae (see pp. 184–187).

Trypanosoma gambiense has a distribution in Africa that closely approximates that of *Glossina palpalis*. Sleeping sickness has been known for nearly two hundred years, and various accounts of its peculiar manifestations were written in the early part of the nineteenth century, particularly by those engaged in the slave trade. The disease was brought over to the West Indian Islands but never became established nor did it spread among the population for reasons now well known. Though restricted at first to an extensive area in West Africa, its distribution throughout that continent began with the commercial development in the eighties of the last century. It is believed that Stanley, the African explorer, brought the disease into the heart of the continent and to the Uganda and Great Lakes region during his trip across from the Congo to the Nile (1887–1889). In 1901 an epidemic of the disease broke out in Uganda, and since that time intensive investigations have been conducted by numerous workers in various parts of Africa.

Sleeping sickness manifests itself in two rather distinct phases—an intermittent fever phase that may last for months or years and the so-called true "sleeping sickness." The first stage is characterized by irregular fever, debility, languor, vague pains, enlargement of the glands of the neck, edematous swellings, and generally an erythematous rash. This condition may continue for months or years (now called "trypanosomiasis" stage) and is practically always followed by the second phase, the "sleeping sickness" stage (due to the invasion of the nervous system). The drowsiness and languor become pronounced, no interest is taken in the surroundings, and no attempt is made to obtain food though the patient will eat if food is offered. The fever continues, wasting becomes pronounced, and the patient passes into a state of coma till death intervenes (Fig. 170).

Although the disease was long known, it was not till Forde observed an organism (which he thought at first was a filaria) in the blood of a European patient in Gambia suffering from a peculiar fever known as "Gambian fever" that led to the discovery of the causative agent. Dutton (1902) saw Forde's preparations and pronounced the organism a *Trypanosoma,* which he later described as *Trypanosoma gambiense*. Castellani (1903), working in Uganda, discovered a trypanosome in the cerebrospinal fluid of natives suffering from sleeping sickness, described it as *T. ugandense,* and asserted it to be the etiological agent of the disease. Bruce and Nabarro (1903) confirmed Castellani's work and also recovered the parasite from the blood in the early and later stages of the disease. It was soon determined that *T. ugandense* was identical with *T. gambiense,* so that the etiological agents of West Coast and central African sleeping sickness are the same. Since then numerous investigators have fully confirmed and extended these results. Bruce and Nabarro (1903), by means of a study of the distribution of the disease and the species of tsetse fly (*Glossina palpalis*) present in the area, concluded that this fly was the agent responsible for its spread. This they confirmed by feeding experiments, transmitting trypanosomes by the fly from patients to healthy monkeys and also infecting monkeys by flies caught in the wild.

Though *Glossina* flies had now been shown to transmit (in practically all experiments probably mechanically though some workers thought there must be a cyclical development in the fly) two species of trypanosomes (*T. brucei* by *G. morsitans* and *T. gambiense* by *G. palpalis*), it was not known what relation these parasites bore to the flies. Kleine (1909) demonstrated that the trypanosomes undergo a cyclical development in the flies and that once a fly is infected it may remain infected for a considerable period. These results have been fully confirmed, adding another link in the etiological chain of this disease. Finally Bruce and his co-workers (1910, 1911) showed the possibility of domestic cattle and wild game acting as reservoirs of *T. gambiense*. Since then, owing to the extreme difficulty of identifying the different species of trypanosomes, many confusing reports on this phase of the parasite's host have been published. It would seem, according to Wenyon (1926), that "occasionally domestic animals living in association with human beings amongst whom this disease occurs may acquire the infection, but there is little or no evidence to incriminate the wild game as reservoirs of this trypanosome."

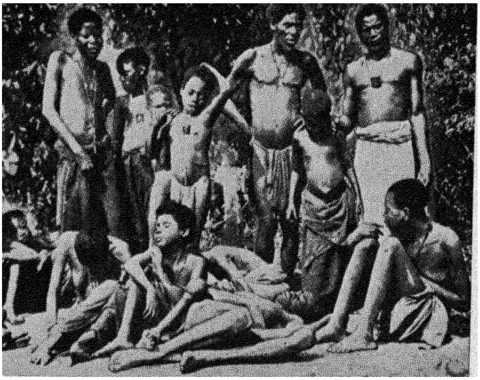


Fig. 170. Sleeping sickness. A group of natives in different stages of the disease. (From Byan and Archibald, *The Practice of Medicine in the Tropics.*)

The cyclical development of *T. gambiense* in *Glossina palpalis* has been most carefully investigated by Robertson (1913). When the fly ingests blood containing trypanosomes, one of several alternatives may occur:

1. All the trypanosomes may be digested in 50 to 72 hours and disappear from the gut.
2. Some of the trypanosomes may persist in the crop and gut but disappear with the next feeding.
3. They may survive in the gut and multiply in the first blood meal even though a second feeding has taken place. These may be swept out when the original meal is digested.
4. Some may persist and develop in the crop with successive feedings, but no infection will occur as there is never a permanent crop infection.
5. Some will persist in the gut after the first meal has been entirely replaced by the second blood meal.

This last condition brings about a permanent infection of the fly. The trypanosomes multiply rapidly and from the tenth to the fifteenth day distinct, slenderer forms arise and almost completely fill the posterior part of the midgut. These push forward to the proventriculus, thence up into the hypopharynx and along the salivary ducts into the salivary glands. Arriving in the salivary glands they gradually change to broad crithidial forms, multiply, and fill up the glandular cavity. Here soon appear stumpy forms, closely resembling the blood type, and these are the infective forms. The entire cyclical development, from the time of the ingestion of blood trypanosomes to the appearance of the infective salivary forms, requires from 20 to 30 days. During this period the fly must have access to blood meals when needed. Once a fly becomes infected it remains so for probably the rest of its life.

In addition to *G. palpalis* the following species have been shown, experimentally, to be capable of transmitting *T. gambiense: G. morsitans, G. pallidipes, G. fusca,* and *G. tachinoides.*

Rhodesian sleeping sickness is caused by *T. rhodesiense* (Fig. 169) which was recognized and described by Stephens and Fantham in 1910. The disease runs a more rapid course and brings about death in a few months (three or four), death usually intervening before the "sleeping stage" develops. The parasite is more pathogenic to laboratory animals, monkeys dying in from 8 to 14 days after infection, whereas with *T. gambiense* death may occur in from 27 to 159 days; in rats, *T. rhodesiense* is extremely virulent, whereas *T. gambiense* produces a chronic infection. Many investigators believe that *T. rhodesiense* is but a strain of *T. brucei* which has become capable of infecting man.

This type of sleeping sickness is rather restricted in its distribution, occurring in parts of Rhodesia, about Lake Nyasa, in the northeast part of Mozambique, and in the southeastern corner of Tanganyika. This disease was shown by Kinghorn and Yorke (1912) to be distributed by *G. morsitans* and confirmed by Bruce and his co-workers (1914). The latter also incriminated *G. brevipalpis.* The developmental cycle of the parasite in the fly is similar to that of *T. gambiense* in *G. palpalis.*

Nagana or tsetse-fly disease of cattle is caused by *T. brucei.* This parasite was discovered by Bruce in 1895, who also showed (1897) that it was transmitted by *Glossina morsitans.* The disease is widespread in Africa, extending from Zululand to the Sudan. *T. brucei* is probably the most virulent of all known pathogenic trypanosomes. It is inoculable into practically all mammals. Horses, mules, donkeys, and camels usually die within a fortnight to three weeks; cattle are not killed so rapidly but very few recover; pigs succumb quickly and dogs die in about two weeks after inoculation; rats and mice are very susceptible, while cats are more tolerant; monkeys, with the exception of baboons, die usually in three or four weeks; many other domestic animals are susceptible, and the disease runs a rather rapid course (Wenyon). Bruce (1895) found what he considered this species in many kinds of wild game and later demonstrated that in Nyasaland nearly 32 per cent of the wild game harbored *T. brucei* or other species pathogenic to domestic animals. This work has been confirmed by other workers and the reservoir of this trypanosome definitely established.

Though this trypanosome is primarily a parasite of numerous species of mammals, man has long been considered immune. Since the discovery of *T. rhodesiense* by Stephens and Fantham, many investigators consider this human species as but a strain of *T. brucei* that has become adapted to man (Wenyon, 1926). Kleine (1923) maintains that *T. rhodesiense* is a distinct species and that its animal reservoir has not yet been ascertained.

The species of *Glossina* flies that are known to transmit *T. brucei* are *G. morsitans, G. brevipalpis, G. pallidipes, G. palpalis,* and *G. tachinoides.*

CONTROL OF *GLOSSINA* FLIES

As no very effective treatment for sleeping sickness of man (except the use of certain drugs, and these do not prevent reinfection or guarantee a cure), nagana of horses, mules, cattle, etc., and other trypanosomiases has yet been devised, the problem of the control of *Glossina* flies is a major one in many parts of Africa. Sleeping sickness has devastated many populous districts (Uganda) of Africa, rendered much agricultural land unfit for habitation, and threatens the future development of some of the most fertile regions of the world. Though extensive investigations have been and are now being carried on, the problem of tsetse-fly control is a baffling one. At the present time much progress has been made in the reduction of *Glossina* flies by some or all of the following methods: (1) by clearing the jungle along the "fly belts," by using the same methods about native villages, and by removing forested areas along water courses (it is only necessary to clear some 50 to 100 yards in these areas as the flies rarely move very far from protected growths); (2) by trapping the flies in those areas where they are numerous, especially near populated districts; (3) by avoiding "fly belts" so as not to introduce the disease into free areas; (4) by wearing white clothing (the flies prefer dark surfaces on which to alight) and by wearing head nets, gloves, and protective clothing; no satisfactory repellent has yet been developed; (5) by constructing better housing, using screens, and improving sanitation; and (6) by destroying game animals. The latter method, though practiced in some districts, does not seem worth while as domestic animals may also serve as reservoirs. However their reduction in populous areas may serve a useful purpose. More recently the use of various DDT formulations in certain areas shows promise.

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CHAPTER XVI

The Housefly and Its Allies[1]

THE housefly (*Musca domestica* Linn.), or the "typhoid-fly" as it is designated by some writers, is the most common and abundant fly in and about homes throughout the world; it is the animal most commonly associated with man; it is distributed from the subpolar regions to the tropics, where it occurs in enormous numbers.

DESCRIPTION: The housefly (Fig. 171) is mouse-gray in general color. The thorax is gray, marked by four equally broad, dark, longitudinal stripes, most clearly defined in front. The abdomen has the sides of the basal half yellowish and somewhat transparent; the posterior segment is brownish black and a dark longitudinal line extends along the middle of the dorsum. The legs are blackish brown. The wings are clear though somewhat yellowish at the base. The venation is rather distinctive (Fig. 172); the fourth longitudinal vein is sharply bent upwards so as nearly to meet the vein in front. The squamae (calypteres) are large, opaque, yellowish. The adult measures 6 to 7 mm. in length with a wing expanse of 13 to 15 mm.

LIFE HISTORY: The housefly undergoes a complete metamorphosis. Mating takes place in from 2 to 12 days after the adults emerge. Oviposition may begin within 2 to 3 days after copulation. The female deposits its eggs singly, laying from 100 to 150 eggs at a time in a batch (Fig. 173). Each female lays several batches, four or more, during her lifetime, that is, from 400 to 600 eggs. Dunn (1923) records remarkable fertility for the housefly in Panama, a single female laying 2387 eggs during a period of 31 days.

The egg is white, oval in shape, and measures about 1 mm. in length. Along the dorsal surface of the egg are two distinct riblike thickenings. The eggs hatch in from 12 to 24 hous (at temperatures of from 68° to 80° F.), though hatching may be delayed by lower, or somewhat hastened by higher, temperatures.

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[1] For the identification of the families in this group of flies, consult the key on pp. 228–231, beginning at No. 11.

The larva (Fig. 173) develops very rapidly when food supply and temperature are favorable. There are three larval stages or instars. The last stage is reached in from four to eight days. The mature larva measures about 12 mm. in length. It is white in color and conically-cylindrical in shape. The body tapers off gradually from the middle region to the anterior or head end. The posterior is cylindrical but the last segment is larger and obliquely truncate. The body is composed of twelve visible segments and is legless. Near the middle of the declivity of the last segment are the posterior spiracles—two D-shaped sclerotized rings placed rather close together (Fig. 195 *4*). Each spiracle consists of a ring that encloses three sinuous slits through which the air passes to the tracheal system. On the inner flat side of the ring is a heavy sclerotized area, the so-called "button." The anterior spiracles are situated laterally at the

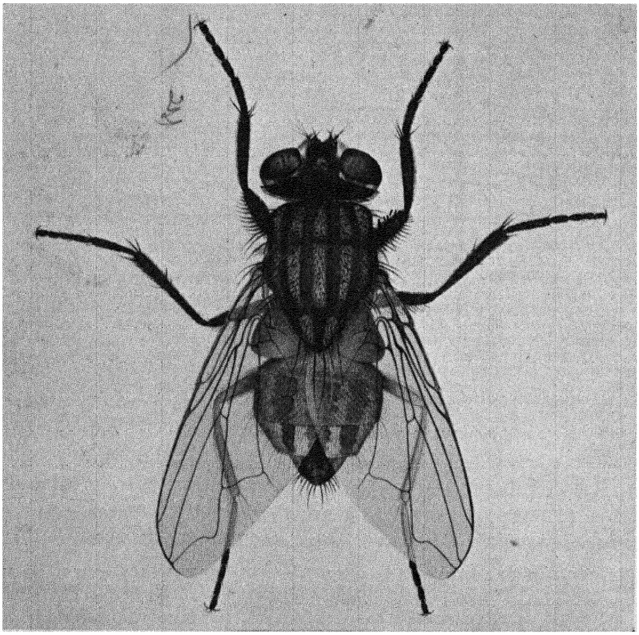


Fig. 171. The housefly, *Musca domestica.* (Courtesy Department of Agriculture, Division of Entomology, Canada.)

posterior border of the third body segment. Each spiracle consists of a fan-shaped body bearing six to eight small papilliform processes.

The larva of the housefly, like all muscid larvae, lacks a true head: the first segment (usually termed the "pseudocephalon") is nearly all retracted within the body. At the anterior end of the larva is seen a heavily sclerotized structure withdrawn within the anterior segments. This structure is the cephalopharyngeal skeleton. It is a part of the head and mouth parts that has become invaginated within the thoracic segments. This structure occurs in all muscoidean larvae and shows numerous modifications. As it is used extensively for identification purposes, a detailed description is here presented (see Chapter xvii for those of other species). Anteriorly may be recognized a pair of oral lobes, each of which bears a pair of sensory papillae (Fig. 174). Between and below the sensory lobes is the mouth opening. On the lateral and ventral surface of these lobes may be noted a series of delicate parallel channels that converge toward the mouth; these have been called "food channels" (Fig. 174 FC). Behind and lying within the thoracic segments is the cephalopharyngeal skeleton. This structure consists of a number of heavily sclerotized sclerites as follows: *Mandibular Sclerite* (MS)—This sclerite has a broad base and bears a pair of mouth hooks. Each mouth hook is shaped like a claw, directed forward and downward; the left hook is much smaller than the right and may be overlooked (the small left hook is found in all species belonging to the genus *Musca*). The larva takes only liquid food and the mouth hooks are employed in tearing and loosening the debris and as an aid in forward movements. *Dental Sclerite* (DS)—At each side of the base of the

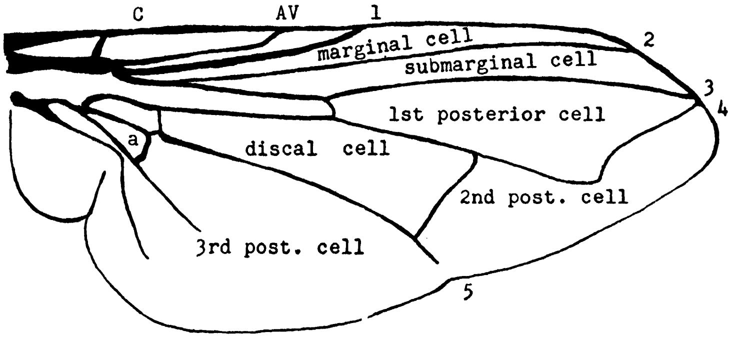


Fig. 172. Wing of housefly; veins and ce labeled. a, anal cell; AV, auxiliary vein; C, costa.

mandibulate sclerite is a small dental sclerite; each affords attachment for powerful muscles which depress the mouth hooks. *Hypostomal Sclerite* (HS)—Posteriorly the mandibular sclerite articulates with the hypostomal sclerite. This consists of two irregularly shaped lateral plates connected by a ventral sclerotized bar. *The Pharyngeal Sclerites* (PhS)—The hypostomal sclerite articulates with the anterior portion of the pharyngeal sclerites. The pharyngeal sclerites consist of two lateral, irregular plates united at their dorsoanterior ends by a transverse sclerite—the dorsopharyngeal sclerite; ventrally the lateral plates are continuous with the floor of the pharynx (Ph). The floor of the pharynx is distinctly grooved longitudinally.

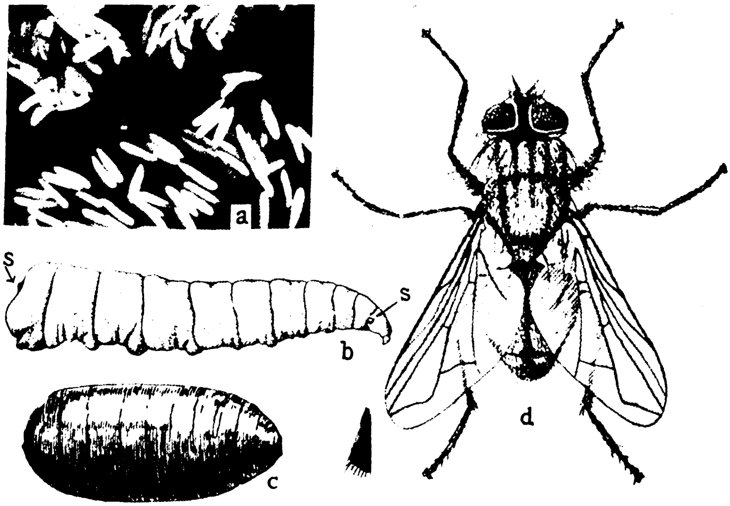


Fig. 173. Metamorphosis of insects. The housefly, *Musca domestica.* (*a*) Eggs as laid in horse manure. (*b*) The full-grown larva (head of larva to right). (*c*) The puparium. (*d*) The adult fly. S, anterior and posterior spiracles.

When the larva is mature it ceases feeding and proceeds to contract. The anterior end is drawn in and within a few hours (6 to 12) a cylindrical case, the puparium, is formed (Fig. 173). Within the puparium the true pupa develops. At first the puparium is creamy yellow in color but it soon changes to a rich, dark brown. Externally nearly all the larval structures, except the cephalopharyngeal skeleton, which is withdrawn within the puparium, may be observed. The pupa develops a new opening to the respiratory system, a pair of small, spinelike projections between the fifth and sixth segments. The puparium averages about 6.5 mm. in length. The pupal period occupies from four to five days, though it may be shortened by high temperatures (90° to 95° F.) or prolonged by cool weather. When ready to emerge the imprisoned fly breaks open the anterior end of the puparium by means of the ptilinum or frontal sac. The puparium splits in a circular fashion in the fifth segment and two lateral slits pass forward from it. The fly works its way out and if the puparium has been formed beneath the soil the fly pushes its way upward by alternately inflating and deflating the frontal sac (ptilinum). The external skeleton soon hardens, the wings become firm, and the fly starts out as a mature insect.

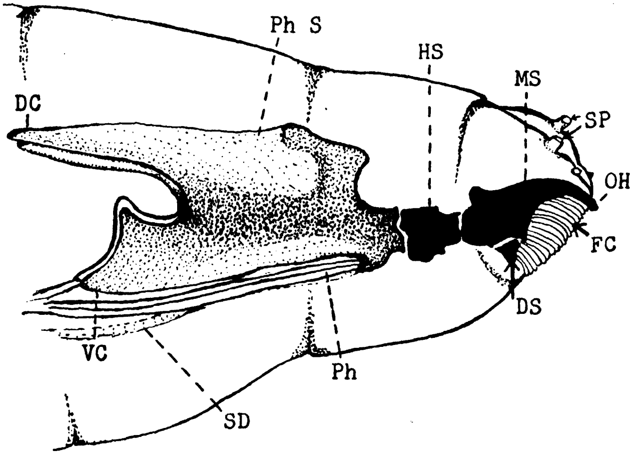


Fig. 174. The anterior end of the larva of the housefly showing the structure of the cephalopharyngeal skeleton. DC, dorsal cornua; DS, dental sclerite; FC, food channels; HS, hypostomal sclerite; MS, mandibular sclerite; OH, oral hook; Ph, pharynx; PhS, pharyngeal sclerite; SD, salivary duct; SP, sensory papilla; VC, ventral cornua.

The entire life cycle from the deposition of the eggs till the emergence of the adults varies widely, due to temperature, food and other factors. Normally it requires from 8 to 20 days. In the warm summer months the average time is from 10 to 16 days. Where conditions are favorable, as in the tropics and subtropics, breeding is continuous throughout the year. Where continuous breeding occurs the number of flies is appalling and they invade every conceivable place seeking food and shelter. Even in the United States and countries generally outside the subtropics where breeding is interrupted by the cold winters, the abundance of houseflies at the end of the summer season makes them a terrible scourge. The excessive numbers are due to its high reproductive capacity and the number of broods. In the region of Washington, D.C., Howard (1917) estimates that there are 10 to 12 generations a season. As each female fly lays from 200 to 600 eggs (a much higher number is recorded by Dunn), the progeny of one female has been estimated to be 1,875,000,000,000 adults at the end of the eighth generation.

HIBERNATION: In the cooler climates the continuous breeding of this fly is interrupted by the winter season. How it passes the winter has been investigated by numerous workers. The results are far from uniform. Hewitt (1914) thought the adults hibernated, seeking out sheltered places in which to pass the winter. The same author (1915) states that the adults do actually hibernate in the region of Ottawa, Canada. He did not succeed in carrying living larvae or puparia through the winter under experimental conditions. Hutchison (1918) concludes from a long series of experiments that, in the region of Washington, D.C., hibernation takes place in the larval and pupal stages in or under large manure heaps, or the species is maintained over the winter by continued breeding in warm places where food (both larval and adult) and shelter are available. He finds no evidence to support the thesis that the adults hibernate from November to April "either outdoors, in protected stables, or in attics or heated buildings." Herms (1923) states, "In hibernation flies may live over winter, i.e., from October to April, which is the case in our Eastern and Central States." No experimental or observational data appear to support the statement of Herms except those of Hewitt. In northern New York (Lake Champlain region) Matthysse found excessive breeding of houseflies in box stalls housing horses during the middle of the winter season. The author made similar observations in box stalls in Nova Scotia years ago. It is probable that breeding continues in many such places throughout the cold weather. The author has frequently found freshly emerged houseflies in cafeterias and similar eating places in winter, indicating local breeding in garbage cans or other refuse.

BREEDING PLACES: The results of numerous investigations clearly demonstrate that horse manure is the favorite breeding ground of the housefly. When horse manure mixed with straw or other refuse is piled in the open, it soon becomes heavily infested with maggots (Fig. 175). The number of flies that may develop in a small manure heap is almost beyond belief. Herms counted 685 maggots per pound and estimated that 900,000 were present in a ton of manure that had been exposed only four days. Howard counted 160 maggots and 146 puparia in four ounces of manure—in other words, a pound of manure could produce 1200 flies and a ton of manure, if heavily infested, could yield nearly 2,400,000 flies every two weeks during the summer months. When it is remembered that manure piles are always present and that the housefly ranges widely, it is not to be wondered that the pest occurs in countless numbers. Not only does the housefly breed in open piles of horse manure but the writer has found them in box stalls where the manure mixed with straw had been allowed to accumulate. In such places, especially near the margins where the manure is not so thoroughly packed, the maggots may be found in countless numbers. In fact, horse manure wherever found, if moist, serves as an ideal breeding ground.

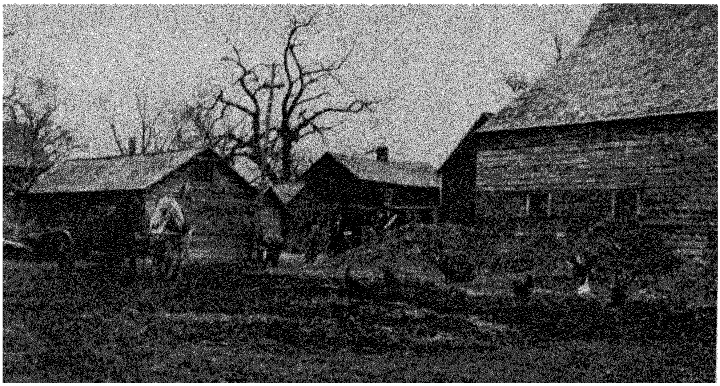


Fig. 175. View of barnyard, showing an ideal place for the breeding of houseflies.

The second most favored breeding place is human excrement wherever exposed, as in open privies, in wooded dell, hillsides, back alleys, and yards. Such exposed human feces are very dangerous breeding grounds as will be shown later. Other breeding grounds are cow manure, especially when mixed with straw and horse manure, manure and wastes about piggeries, decaying animal and vegetable wastes where fermentation occurs, piled decaying vegetables, so-called "septic tanks" (the cracks between the covering boards furnishing the entrances and exits for the flies), and, most fruitful of all breeding grounds, the garbage dumps of many of our cities and larger villages. A visit to a garbage dump will soon convince any intelligent citizen that he is paying out money to provide breeding places for flies that invade his home, defile its cleanliness, contaminate his food, and distribute diseases. Other extensive breeding places are found wherever feed grain or other foods are scattered such as beside or under slatted walks, at loading and unloading platforms, and in similar places where rain soon produces ideal conditions for the larvae. Urine-soaked soil and places about homes where greasy wastes are dumped about buildings are other favorite spots. In conclusion it may be said with fair accuracy that the housefly will breed in practically all decaying and fermenting animal and plant wastes.

HABITS OF THE ADULTS

The housefly is, above all things, a lover of human and animal habitations. The identification of all flies captured in households (over 200,000 have been identified) shows that about 90 per cent of them consist of the housefly. The maximum abundance of flies in homes occurs toward the end of the summer season when they seek warmth and shelter as well as food. They are constantly on the move, exploring every surface, seeking food in every conceivable place, and leaving their wastes on every object.

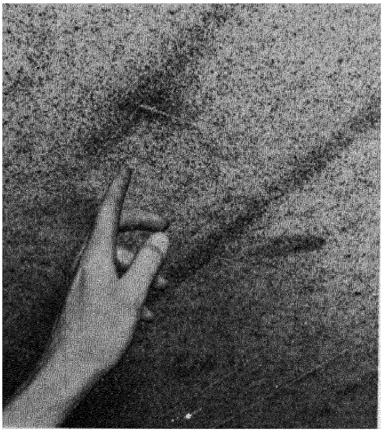
FOOD AND FEEDING: Its principal foods are liquids such as syrups, milk, water containing proteins, sugars, moisture on decaying fruits, sputum, fecal wastes—in fact, any substance however vile if it is moist or can be dissolved. It also seeks food on moistened surfaces as about the mouth, nostrils, eyes, sores, and wounds of man or animals or exposed meat, cheese, or other foods. The method of feeding needs to be well understood as it is of great significance in the carriage of pathogenic bacteria and parasites. The mouth parts are fully explained and illustrated in Chapter v, and the method of feeding is described. The fly, undisturbed, can fully engorge in less than half a minute. On a substance such as dry sugar, sweetened cakes, dry blood, sputum, etc., the fly dissolves it first by secretions from the lingual salivary glands and, frequently, by regurgitating a part of the liquid present in the crop. This habit of regurgitating is especially noticeable after the fly has fed on liquids (Fig. 50). Furthermore this habit of regurgitation is commonly employed on nearly every surface the fly tests with its proboscis, leaving as a result light-colored opaque spots—the so-called "vomit spots." Such spots are frequently more common on windows, ceilings, etc., than the fecal spots. The regurgitation from the crop does undoubtedly serve in the spread of pathogenic as well as nonpathogenic organisms. These methods of feeding make the housefly a serious menace, for it may quickly pass from fecal wastes, vomits, exposed sores, and wounds directly to the daintiest foods and liquids of all kinds and pass on either by its vomit spots or fecal wastes a part of whatever has been engorged.

In addition to its feeding habits the housefly possesses an ideal hairy body and legs to which all sorts of germs may adhere as it wallows over the most filthy of animal fecal wastes, garbage, soiled food, etc. Furthermore, its feet (six of them) are each provided with two flattened pads (Fig. 54). These pads (pulvilli) are thickly beset with tiny hairs from which a sticky substance exudes enabling the fly to walk on glass, on ceilings, and similar places, and to gather up or leave behind any filth that it may have garnered in its travels. Such flies frequently fall into our milk, drinks of all kinds, jams, etc., and distribute what they have collected.

FLIGHT: The housefly is a vigorous flier and can travel considerable distances. From the standpoint of fly control and the dispersion of fly-borne diseases the flight range is very important. In other words, can a small area such as a village or city conduct intensive campaigns for the destruction of breeding grounds and thereby hope to remain free from flies? Or, in rural communities, can individual farmers or small communities control flies and remain free from migratory hordes coming from not far distant breeding grounds? Furthermore, if the housefly is a wide-ranging species its possibilities of distributing disease-producing organisms are greatly increased. Until 1916 the maximum flight range was considered not over a mile, and this conclusion was based on experiments conducted in England. In that year Parker in Montana demonstrated, largely under city conditions, that the fly travels nearly two miles and in considerable numbers. Recently Bishopp and Laake (1921) carried out an extensive series of flight experiments in Texas. The flies were captured, dusted with finely powdered red chalk or paint, and then liberated in the open fields. In all, some 234,000 flies were used in these experiments. The results are very significant. Within 24 hours after liberation the housefly was captured six miles distant from the point of release, and the maximum distance traveled was 13.14 miles by one female. Considerable numbers of the flies were recaptured at the traps at ranges of five, six, and eight miles, showing conclusively that the housefly migrates long distances within comparatively short periods of time. From the point of release the flies tended to migrate with the prevailing winds, but they also spread at right angles to, and even against, the wind. These investigators concluded that moderate winds have little influence in directing the spread of flies.

RESTING PLACES: As the control of houseflies by DDT seems very effective, it is of some importance to recognize their selective resting places at night or on dark days so that treatment may be directed to those particular places. In barns and buildings of all kinds, including our homes, flies seem to seek out cracks and crevices (Fig. 176) such as those behind moldings and in wallpaper, boards, and plaster for resting. This is shown by the dense fecal wastes in those places. Adequate treatment of such areas may be just as, or more, effective than a general over-all treatment with DDT.

LONGEVITY: That the housefly can survive long periods if food and shelter are adequate has been demonstrated many times. Flies reared experimentally in the autumn or winter have been kept alive for many weeks—over eleven by Jepson (1909). Hewitt was unable to keep them alive longer than seven weeks. Herms in California records an average life period of 30 days, with a maximum of 60 days in the summer. Under experimental conditions during the summer at Ithaca, New York, individual flies have been fed and kept alive for from 30 to 70 days. It is evident, therefore, that the housefly lives, on the average, at least a month during the summer and rather longer during the cool months if food and shelter are provided.



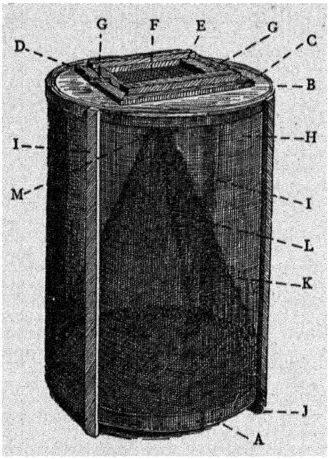


Fig. 176 (left). Resting place of housefly. Note the dense fecal wastes along the cracks. (Courtesy Federal Research Administration, H. I. Scudder.)

Fig. 177 (right). Conical hoop fly trap, side view. A, hoops forming frame at bottom; B, hoops forming frame at top; C, top of trap made of barrel head; D, strips around door; E, door frame; F, screen on door; G, buttons holding door; H, screen on outside of trap; I, strips on side of trap between hoops; J, tips of these strips projecting to form legs; K, cone made of tin or screen wire; L, united edges of screen forming the cone; M, aperture at top of cone. (From Bishopp.)

THE HOUSEFLY AND DISEASE

That the housefly is an active and important carrier of bacteria, certain Protozoa, and the eggs of helminths (round- and flatworms) has been demonstrated by extensive experimental work by numerous investigators. Furthermore it serves as an intermediate host in the developmental cycle of certain parasitic worms. In general houseflies affect the health of man and animals in the following ways:

1. By their annoying habits and excessive numbers they irritate and reduce the vitality of man and animals. This is especially true for children, old people, persons suffering from nervous disorders, or those sickly and delicate. In the case of domestic animals, Freeborn and Bishopp have also shown that an excessive number of flies causes a marked reduction in milk flow in cows.
2. By means of their hairy bodies, their feet well provided with sticky pads, and their feeding and egg-laying habits, they serve as ideal mechanical distributors of filth containing bacteria, protozoan cysts, and helminth eggs to man's food and directly to his person, especially about his mouth and eyes where they constantly seek moisture.
3. As the housefly feeds on all kinds of fecal material, especially human; decaying animal and plant substances; infected liquids, as milk and water, it can take into its intestinal tract all sorts of bacteria, protozoan cysts, and certain helminth eggs, and distribute them in its feces or by way of the vomit spots. It has been shown by many workers that certain of these organisms pass through the fly's intestine in a viable condition. It has also been shown that the maggots feeding on infected fecal material take in certain bacteria and pass them on through the pupal stage to the adults. Experimental evidence indicates that this method of transfer of pathogenic organisms is rather uncommon.
4. The housefly serves as an intermediate host in the life cycle of certain parasitic helminths.

ORGANISMS DISTRIBUTED BY THE HOUSEFLY

As a mechanical distributor of germs the housefly probably has no equal. Cox, Lewis, and Glynn (1912) showed that flies from sanitary areas carried externally much smaller numbers (21,000 to 100,000) of bacteria per fly than flies from unsanitary areas (800,000 to 500,000,000 per fly). Torrey (1912) obtained similar results. In the fly's intestinal tract the abundance of bacteria is astounding, owing, no doubt, to its varied feeding habits. Torrey states that the bacteria of the intestinal tract are 816 times as numerous as those upon the external surface of the fly. Cox, Lewis, and Glynn report numbers of bacteria in the intestinal tract varying from 10,000 to 333,000,000 per fly from unsanitary areas and only 100 to 10,000 per fly caught in sanitary districts. Scott (1917), working in the District of Columbia, reports much fewer bacteria carried externally per fly and confirms the previous workers' results that flies from sanitary areas carry fewer organisms than those from unsanitary areas.

The danger from flies is their habit of wallowing and feeding in all sorts of fecal matter, decaying wastes, etc., and then flying directly, or within a short period, to human food, depositing thereon their fecal wastes and vomit spots, or contaminating it by germs carried externally. Though much work has been done in an effort to determine the organisms distributed by flies, the results are not as extensive as is frequently believed. The problem is an extremely difficult one. However, the following known pathogenic bacteria (the list is not intended to be complete) have been isolated from the housefly.

Bacillus typhosus[2] by Hamilton (1903), Fickler (1903), Faichne (1909), Brterelli (1910), Graham-Smith (1910), Cochrane (1912).
Bacillus paratyphosus "A" by Torrey (1912).
Bacillus paratyphosus "B" by Nichol (1911).
Bacillus dysenteriae (Morgan's organism) by Morgan and Ledingham (1908–1909).
Bacillus dysenteriae (Flexner type) by Graham-Smith (1909), Manson-Bahr (1910), and others.
Bacillus coli (and its many varieties) by various investigators.
Bacillus enteritidis (?) by Torrey (1912).
Bacillus tuberculosis by Spillman and Haushalter (1887), Hoffman (1888), Hayward (1894), Lord (1904), Graham-Smith (1910), and others.
Bacillus pestis by Yersin (1894), Nuttall (1897).
Bacillus cuniculicida by Scott (1917).
Bacillus anthracis by Graham-Smith (1910, 1911, 1912).
Bacterium tularense by Wayson (1914).
Brucella abortus by Nishimote (1931, unpublished).
Staphylococcus spp. by many workers.
Streptococcus spp. by various workers.
Spirillum cholerae (*Vibrio comma*) by Tizzoni and Cattani (1886), Simmonds (1892), Graham-Smith (1910).

Though many other species of bacteria have been reported from the housefly, it would seem that this entire field should be carefully restudied, using the newer and more exacting technique of present-day bacteriologists and giving more attention to the specific types of bacteria.

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[2] The names of bacteria employed here are those that appeared in the original papers. The present names can be found in any modern textbook of bacteriology.

Cysts of the following human intestinal Protozoa have also been reported taken up by the housefly and passed in its feces in a viable condition: *Endamoeba histolytica, Endamoeba coli, Giardia intestinalis* (by Wenyon and O'Connor, 1917; Roubaud, 1918; and Root, 1921), and *Chilomastix mesnili* (Root, 1921). These cysts do not persist alive within the fly's intestinal tract for any great length of time, usually not longer than two or three days. However, they are passed in a viable condition during this time and may be deposited in milk, on moist foods, or in water. Furthermore, Wenyon and O'Connor recovered the cysts of *E. histolytica, E. coli,* and *Giardia intestinalis* in the feces of flies caught in the wild. What importance can be assigned the housefly as a distributor of Protozoa is still unsettled and further work along this line is needed. Frye and Melaney (1932) report finding the cysts of *Endamoeba coli, E. histolytica, E. nana,* and *Giardia* in flies caught in houses where carriers were present. None were found in flies taken out of doors.

As an intermediate host in the developmental cycle of helminths the housefly plays no mean part. As yet our data are far from complete but the following species are known to pass certain stages in the fly: *Choanotaenia infundibulum, Davainea tetragona, Davainea cesticillus, Habronema microstoma, Habronema megastoma,* and *Habronema muscae.* As a result of his experimental work Nicoll (1911) found the fly capable of ingesting and passing in a viable condition the eggs of the following species: *Taenia solium, Taenia serrata, Taenia marginata, Hymenolepis nana, Dipylidium caninum, Oxyuris vermicularis,* and *Trichuris trichiura.* Externally the fly may distribute from fecal wastes any eggs that may adhere to its hairy body or feet. These can be deposited in liquids, foods, or other material eaten or handled by man.

SPECIFIC DISEASES

TYPHOID FEVER: As already pointed out, the housefly acts as an efficient carrier of many of the colon-typhoid bacilli. Typhoid and the paratyphoid fevers are caused by *Eberthella typhosa, Salmonella paratyphi* (*B. paratyphosus* A), and *S. schottmülleri* (*Bacillus paratyphosus* B). These organisms are primarily parasitic and according to Jordan (1929) are found outside the human body "only in those situations where it could be more or less directly traced to an origin in the discharges of a typhoid patient or convalescent." In pure water the life of typhoid bacteria appears to be rather short, probably not over a month, and there is no multiplication but, on the contrary, a steady decline in their numbers as time goes on. Human infection from water is to be feared chiefly when there is fresh sewage contamination; undoubtedly the principal typhoid epidemics have been traced to polluted drinking water. In the human body the typhoid organisms are present principally in the intestine, urinary bladder (at least 25 per cent of all cases; Jordan, 1929), kidneys, and the blood stream. In the kidneys the infection may be intense (100,000,000 to 500,000,000 bacteria in a single cubic centimeter of urine) and be prolonged for weeks and months after recovery. The same holds true for the gall bladder infections. In addition, a small percentage (0.5 to 11.6 per cent or even as high as 25 per cent) of those who recover from typhoid fever became "chronic carriers" or "permanent carriers," that is, they continue to pass the bacilli in their feces or urine for considerable periods—six months (chronic carriers) or during their lifetime (permanent carriers). From this hasty survey it will be seen that the typhoid bacilli are discharged from the human patient and "carriers" in the urine and feces so that the ground about open privies, soil or water polluted with sewage, etc., may and do serve as foci for the further spread of the disease. Here we are only interested in the part played by the housefly in the spread of the disease. Houseflies are constant visitors to sewage wastes and to exposed human feces, on which they feed and oviposit; they also are attracted to urine and frequently breed in soil saturated with urine. From such filth they pass directly to our food, deposit their feces and vomit spots thereon, or fall into milk, sweetened liquids, jams, etc., and may leave behind large numbers of the typhoid bacilli.)That flies carry these bacilli has been proved a number of times, and Hamilton (1903) has shown experimentally that living bacilli may remain in or on the body of the fly for at least 23 days after contamination. Reed and his associates (1900) present the most extended investigations of fly carriage of typhoid in their study of the severe outbreaks of the disease among American troops during the Spanish-American war. Jordan (1929) states that "cases formerly attributed to air-carriage may perhaps be more reasonably ascribed to the agency of flies." Sweet (1922) states that flies are in part responsible for the spread of typhoid fever. "In the United States alone during 1920 over 8000 persons died from typhoid fever, and ten times that number suffered from the infection, the rate being several times higher than that of many civilized countries." From these and numerous other investigations it is safe to conclude that flies are an important agency in the dissemination of typhoid fevers. (As most of the positive findings of flies harboring typhoid baccilli were made before our present fuller knowledge of the disease, it would seem that the earlier work ought to be confirmed or disproved by modern techniques.)

DYSENTERY: Two distinct diseases are indicated under this term: bacillary dysentery caused by *Shigella* (*Bacillus*) *dysenteriae* and *S. paradysenteriae* and amoebic dysentery caused by *Endamoeba histolytica.* These organisms have been shown to be carried by flies and distributed either by way of their feces or vomit spots.

Bacillary dysentery is frequently a scourge in armies, prisons, camps, and military barracks. Not infrequently epidemics occur in the Tropic, Temperate, and even in the Arctic zones. The spread of the disease is due to direct or indirect contact with the fecal wastes of those afflicted. Furthermore, about 3 per cent of those recovered may continue to pass the bacillus in their stools and are thus dangerous individuals in the community. Flies play an important part as indirect distributors of the bacilli, feeding on infected fecal wastes and then contaminating human food. The bacilli have been shown to survive for at least five days in the intestinal tract of flies. Manson-Bahr (1924) states that "the seasonal incidence of bacillary dysentery corresponds in a remarkable manner with the maximum prevalence of these pests (houseflies)."

In amoebic dysentery the organism *Endamoeba histolytica* is discharged in the stools in the precystic or cystic stage. As *Endamoeba histolytica* may not, in many people, produce clinical symptoms of disease, we have what are called "contact" and "convalescent" carriers. As normally 5 to 10 per cent of the average population may be infected, there are large numbers of contact carriers. Persons who have had the disease and have recovered are known as "convalescent carriers." Such carriers, unless effectively treated, may continue to pass the cysts for many years. From these two sources fecal-feeding flies may easily obtain the cysts from exposed excrement, untreated sewage wastes, etc., and distribute them to our food, water, or milk.

In addition, a disease of infants, known as "summer diarrhea," is frequently all too prevalent. The inciting agent is apparently *Shigella* spp. *Shigella dystenteriae* has been found associated with numerous cases but is not invariably present; other intestinal bacteria undoubtedly play a part in the causation of the disease. Flies are generally accused of acting as important distributors of the causative agents of the disease and should be regarded with suspicion until shown otherwise. All stools, vomits, and wastes from infants suffering from the disease should be disinfected and at all times protected from flies. In preventing the spread of the disease the protection of infants and their food from flies is of extreme importance. Martin (1913), after analyzing all the factors involved in the spread of summer diarrhea, concludes that the carriage by flies may not be the dominant one but probably is one of the most important. Armstrong (1914) clearly shows an increase of the disease among infants in an unprotected, congested, unsanitary area in New York City as compared with a fly-protected, more sanitary area in another congested district of the same city. Recent experimental work by Watt and Lindsay (1948) indicates that diarrheal diseases can be reduced in high morbidity areas by the efficient use of DDT. However the authors conclude that the cost of eliminating the worst fly-breeding places is less and the results more effective than the use of DDT. In other words, good sanitary measures cost less in the long run and are permanent, whereas the use of DDT is a temporary expedient.

CHOLERA: Cholera is an acute disease caused by *Spirillum cholerae* (*Vibrio comma*). The organism is discharged in the stools of the patients and infection takes place only through the contamination of food or water or by direct contact. In the dejecta of cholera patients the vibrios may live for days in soiled, damp linen, for months in water or damp soil. Again a certain percentage of recovered cases harbor the germ in their intestines and act as carriers. From such sources fecal-feeding flies can obtain the vibrios and pass them on through their feces or vomit spots directly to food or drink. The vibrios of cholera were early shown to be carried by flies. Simmonds (1892) captured flies in a cholera post-mortem room and obtained colonies of the vibrios from them. Graham-Smith (1910) experimented with flies and obtained the vibrios from the legs up to 30 hours after contamination, from the intestine and crop for 48 hours after infection. These findings have been confirmed by other workers and various observers have recorded their belief that flies are active agents in the spread of cholera epidemics. Patton (1930) doubts that flies play any active part in the spread of cholera. Recently Gill and Lal (1931) presented a new and rather startling hypothesis of fly carriage of cholera. The vibrios were found capable of surviving in the fly for at least five days; in other cases the vibrios apparently disappeared from the gut after 24 hours or so and reappeared on or about the fifth day, at which time the flies are capable of infecting food or drink by their feces (the authors tentatively suggest a definite host-parasite relationship in this case). They also showed that infection of milk by the proboscis can take place up to 24 hours after infection, but they have no evidence that proboscis infection may occur on and after the fifth day.

ANTHRAX: Anthrax is primarily a disease of cattle and sheep caused by *Bacillus anthracis.* Man becomes infected mainly through abrasions of the skin (*malignant pustule*), the organism coming from various sources as infected cattle, sheep, or their products. That flies may act as carriers has been demonstrated by Ballinger, Buchanan, Graham-Smith, and others. As *Bacillus anthracis* is a sporeforming bacillus, it can be easily distributed. Graham-Smith has shown that flies fed on the spores may contain living spores in their intestinal tract for at least 14 days and on their bodies for 20 days. Dried feces and vomit spots contained viable spores for 20 days. He also showed that when larvae were fed on the spores a large proportion of the adults from these larvae were infected(As the spores of anthrax remain viable in the soil for many years (at least 30), flies may obtain them in various ways while feeding on fecal wastes, polluted water, etc. Man may become infected through the deposition of such spores on his food, or, more probably, on exposed sores, wounds, etc) What actual part flies (nonbloodsucking flies) may play in the spread of this disease among domestic animals is not known.

YAWS (Framboesia, Tropical Ulcer): This disease, caused by *Treponema pertenue,* is widely distributed throughout the tropical and subtropical regions. It is very prevalent in many of the West Indian islands and parts of South America and has been reported from the southern United States. The disease is characterized by ulcerous papules which form funguslike, encrusted, granulomatous eruptions, which may extend all over the body. The spread of the disease is mainly by direct contact from person to person. However, flies have been incriminated, and Castellani and Chalmers state that flies eagerly crowd upon the open sores, even in the hospitals, when the dressings are removed. Castellani has recovered the spirochete from houseflies allowed to feed on the scrapings from the sores, and he was able to infect monkeys by placing flies on the scarified areas on the eyebrows. When the excessive abundance of flies in tropical countries is taken into consideration, it would seem that houseflies, flesh flies, and other flies (as *Hippelates* spp., family Chloropidae) must play a part in its distribution.

CONJUNCTIVITIS (Ophthalmia): There are many eye diseases, caused by various agencies. In the spread of some of these, flies are undoubtedly concerned. In many parts of the tropics as China, India, Egypt, sections of South America, and Porto Rico trachoma of the eyes is very prevalent. The housefly is a constant menace on account of its abundance and its persistent efforts to obtain moisture and secretions, purulent or otherwise, from about the eyes. Elliott (1923) states that swarms of flies may be seen alighting on the eyes of people suffering from ophthalmia and they readily pass on the infection to the next healthy conjunctiva on which they alight. "Flies are a great danger as they carry discharges from morbid to healthy eyes" (Elliott). Similar conclusions are stated by Castellani and Chalmers. As early as 1888 Howe stated that the number of cases of conjunctivitis in Egypt increased in proportion to the increase of flies. As far as the writer is aware there are no specific investigations dealing with muscid flies as agencies in the spread of eye diseases in temperate climates. When one witnesses the abundance of flies about exposed babies, persons with eye diseases, etc., it would seem that such insects must play a part not as yet well known.

POLIOMYELITIS: In recent years because of the accumulated knowledge of this disease the common house-frequenting flies rather than the bloodsucking flies have been incriminated as possible vectors. Paul *et al.* (1941) report transmission to monkeys from flies (1000 to 1200 collected at a camp kitchen in Connecticut, where cases in children were present) macerated and injected into a cynomologous monkey. Similar results were obtained from flies caught near a privy in Alabama where cases of polio had recently occurred. Sabin and Ward (1941) also demonstrated the virus in flies taken from urban places in Cleveland and Atlanta where human cases were present. These data were based on infections of cynomologous monkeys injected intraperitoneally with macerated flies. Unfortunately in all these experiments a variety of flies were employed so that it is not possible to say which species carried the virus. However, all of them normally occur about houses; most will feed on fecal wastes, sewage wastes, and human food; and the results demonstrate that flies do carry the virus. Toomey *et al.* (1941) report obtaining the virus from flies taken at the outlet of raw sewage near where the disease was present. Ward *et al.* (1945) demonstrated that food such as bananas exposed to flies in and about homes where polio was present became infected and produced subclinical cases of polio when fed to chimpanzees. Furthermore, the feces of these test monkeys showed the presence of the virus for one or two months after the last feeding. According to Bang and Glaser (1943), the housefly (*Musca domestica*) retained Theiler's mouse "poliomyelitis" as long as 12 days after being infected by feeding but the mouse-adapted human strain survived only two days.

OTHER DISEASES: Flies have been reported as spreading other diseases (plague, tuberculosis, smallpox, leprosy, etc.), but the importance of this means of distribution is probably not great or has not been fully investigated. This may be said especially of tuberculosis. Though the tubercle bacillus is taken up from sputum, intestinal wastes, exudates from tubercular sores, etc., and is known to pass through the fly's intestine in a viable condition for at least a week, we know practically nothing of the part played by flies in the spread of the disease. Their role may be of more significance than is generally conceded, especially when some of the recent work on the presence and viability of *B. tuberculosis* is considered. Brown and his co-workers (1916) recovered viable bacilli in a sewage-contaminated stream three and one-half miles below the outfall; Conroy, Conroy, and Laird (1921) demonstrated living bacilli in the effluent from an Imhoff tank at a sanitarium; Cummins and Ackland (1929) found them in a thin coating over stones at the point of escape of the effluent from a septic tank; Williams and Hay (1930) demonstrated living and virulent *B. tuberculosis* (*bovinus*) in cow manure exposed in the south of England for five months in winter, two months in spring, two months in summer, and four months in autumn. In manure protected from sunlight the organism lives at least four months in summer; in liquid cow manure the bacillus lived for at least four months. The recovery of viable tuberculosis bacilli in such situations clearly indicates ideal sources where flies may obtain them either by feeding or during larval development.

OTHER COMMON HOUSE-FREQUENTING FLIES

Besides the housefly (*Musca domestica*) other species of *Musca* flies are found frequenting the home. *Musca nebulo* and *M. vicina* are the most common bazaar- and house-frequenting flies in India; *M. sorbens* is a house visitor throughout the Netherlands Indies; other species occur in the Ethiopian and oriental regions but do not appear to be serious pests about homes. Other important flies are the lesser housefly (*Fannia canicularis,* Fig. 196), the latrine fly (*Fannia scalaris*), the nonbiting stable fly (*Muscina stabulans,* Fig. 192), the biting stable fly (*Stomoxys calcitrans,* Fig. 166), the "blowflies" (*Calliphora* spp.), the green-bottle flies (*Lucilia* spp.), and the cluster fly (*Pollenia rudis*). The species of "blowflies" and green-bottle flies (*Calliphora* spp. and *Lucilia* spp.) may also act as mechanical vectors of many of the disease-producing organisms in the same manner as the housefly. They are not, however, such invaders of our houses, but in slum districts and badly sanitated areas they may prove important vectors, as shown by Yao *et al.* (1929) in Peiping, China, and by other investigators in different areas. Most of these flies except the last one are discussed in Chapter XVII, to which the reader is referred.

Though the larvae of these flies (except the species *Pollenia rudis*) occasionally cause myiasis, they are also of some importance as nuisances about the home and as mechanical carriers of pathogenic organisms. In general, however, it may be said with certainty that in nearly all cases the common housefly constitutes over 90 per cent of the fly population in houses. The cluster fly (*Pollenia rudis*) is found invading houses only in the autumn. In many places it is veritable pest. The adult closely resembles the housefly in size but is more sluggish. The thorax lacks the light and dark lines and bears many short, golden hairs. In the larval stage it is parasitic on certain species of earthworms. The abundance of the adults largely depends on the availability of the larval host. As no very effective method of reducing the numbers of earthworms is known, we cannot control the fly in the larval stage. As the adults enter our houses in order to hibernate, their presence is only noted in the autumn and again in the spring when they leave their hiding places. In the fall they invade every corner and darkened retreat, where they gather together, often in immense clusters. They may be found in every crack and crevice, crawling sluggishly about. The most effective control is to "swat" them, to spray with Flit, or, better, to use DDT as for houseflies, carefully spraying all their resting places.

THE CONTROL OF FLIES

As the housefly constitutes the major part of the fly population of our homes and is a constant menace to our health and happiness, any sanitary measures required for its reduction ought to be welcomed and carried out with alacrity. Furthermore, it is the most abundant species in our food and bakery shops, in city markets, in candy and delicatessen stores, in meat markets and packing establishments, in and about dairy buildings and milk establishments of all kinds, in public and private toilets, in open privies (especially about rural homes and camp sites), and in our public parks and playgrounds where thousands and tens of thousands of our people congregate.

In order to realize the problem of the control of the housefly it is necessary once again to indicate its breeding places. It breeds most abundantly in horse manure (Fig. 175), in human excrement, decaying vegetable and animal matter of all kinds where fermentation is taking place, in garbage cans and waste, in city dumps and cesspools, in ground saturated with urine and fecal wastes, in poultry wastes, hog pens, dairy wastes, and cow manure mixed with straw or horse manure, in wastes from slaughter houses—in fact, in nearly all places where animal or plant substances decay and fermentation takes place. It is thus clear that the prevention of fly breeding is primarily a problem of sanitation and cleanliness. As the housefly has an extended range of flight, at least 10 or 12 miles, the prevention of fly breeding is a community problem.

The main essentials in fly control may be briefly summarized:

1. By suitable sanitary measures eliminate as many of the breeding grounds as possible at a minimum expenditure of time and money.

2. Destroy the eggs and larvae in the breeding grounds that cannot be eliminated.

3. Where the previous methods cannot be effectively carried out, the following palliatives should be employed in order to reduce the number of adults: (a) The effective use of screens on all doors, windows, or other openings through which flies may enter. (b) The use of DDT as a residual spray. This is, at present, the most satisfactory treatment. (c) The employment of fly and larval traps. (d) The use of fly papers, poison, and "swatting."

SANITARY MEASURES

With the rapid development of city, town, and county public health activities, the education of the general public to adopt effective sanitary measures ought not to be too long delayed. Yet despite educational propaganda by means of health units, the public schools, the radio, etc., we find some of the worst sanitary conditions in our largest cities, in public and private institutions, in our schools, colleges, and universities, in our great public parks, and even in our homes. Cleanliness and the love of cleanliness may be on the increase but the appearance of great filthy "dumps" near cities and villages, great rivers polluted with sewage wastes, harbor fronts reeking with rotting garbage, widespread carelessness in the disposal of wastes, etc., make one dubious. In cities and villages the problem of effective control of flies is comparatively simple as compared with the rural one. The following should reduce fly abundance in cities:

1. An efficient sewage-disposal system—meaning by that a system providing for the receival, treatment, and discharge of all sewage wastes in such a manner that no opportunity for fly breeding can occur.

2. A garbage collection system that compels the individual householder to sterilize the cans thoroughly each week or to dry all wastes and place them in the cans securely wrapped in paper. Only tightly closing cans of heavy construction should be used. Collections should be made once or twice a week in the North and, if possible, five or six times a week in the South (referring to the Northern hemisphere). Garbage cans should be handled with care and not thrown about as if they were only intended for destruction. A well-trained collection crew is essential so that garbage is not spilled about private homes or scattered indiscriminately about the streets and alleys.

3. The effective disposal of such garbage collections, preferably by incineration. Where incineration cannot be employed then a sanitary "dump" may be devised. A sanitary dump is feasible and can be seen in certain cities. In such

cities the ashes are collected separately; they must be free from all garbage. During the winter the ashes may be piled in large heaps on the dump. The garbage is then disposed each day along the front of the dump, covered with ashes, and treated with an effective disinfectant and deodorant. (These are now obtainable and at reasonable prices.) In warm climates the problem is more difficult but it is not unsolvable. The daily application of a 5 per cent DDT spray on the dump will prove very effective.

4. Proper treatment of the garbage-collecting wagons. They should be thoroughly cleaned, washed, and treated with disinfectants and deodorants each day after the close of work. An up-to-date storage and rest room with bathing and cleaning facilities should be provided for the collection crews. And, most essential of all, the person in charge of such work should be thoroughly imbued with one ideal, cleanliness.

5. An alert and well-trained sanitary corps to deal promptly and effectively with all problems arising from the disposal of wastes and the maintenance of conditions inimical to the public health.

6. The effective disposal of all manure from horses, cattle, and other animals kept in cities (see below).

7. Spraying with DDT during World War II for the control of mosquitoes, lice, bedbugs, and other insects has shown DDT to be the most effective agent in the control of the adults of the housefly. It is not of any value in destroying the larvae. To control the housefly it is employed as a residual spray. It should be applied as a 5 per cent (by weight) spray (kerosene solution or xylene emulsion) to all indoor surfaces so as not to "run-off" but leave a residue of at least 200 mgm. per square foot, that is at least 1 gallon of the mixture to 1000 square feet. Also all screens, the framework of doorways and cellar entrances, and other exposed place where flies congregate should be treated. In barns, privies, and outbuildings of all kinds where it is not so necessary to leave no visible deposit, an emulsion or wettable powder suspended in water may be employed. In using this material either employ a professional operator or be careful to follow the directions of the manufacturer or the advice given by your health department, experiment station, or the national health agencies.

Under rural conditions the problem of fly control and the adoption of sanitary measures for the prevention of fly breeding are more difficult. The farmer must maintain domestic animals and conserve the manure supply for the growing of crops. Cleanliness and effective screening are the most available means together with the effective use of DDT. However, the individual farmer, though clean and most exacting in carrying out sanitary measures, may suffer from the carelessness of his neighbors. Under farm conditions the most effective measures may be summed up as follows. (The efficient and careful use of DDT may render some of these measures unnecessary.)

1. An efficient disposal system for all manure, especially human excrement. Indoor toilets with septic tanks are well known and full instructions for their installation can easily be obtained from health departments or frequently from the state agricultural colleges. Where these cannot be installed, sanitary outdoor privies can be constructed or the "chemical" treatment of fecal wastes may be employed.

2. Manure of domestic animals should be disposed of daily where possible, the manure being distributed on the fields, preferably with a manure spreader. When this can be practised, cleanliness is essential—no left-overs in stables, drains, corners, carriers, dump carts, or other vehicles used in the disposal. Such a procedure is costly on the average farm, where manure is usually piled either directly outside the barns (Fig. 175) or placed in concrete pits to await future disposal. In such cases fly breeding may be prevented by one of the following treatments, recommended by the United States Department of Agriculture:

Hellebore may be used at the rate of 0.5 pound to 10 gallons of water. Stir the powdered hellebore in the water and allow to stand for 24 hours. This mixture is sufficient to treat 10 cubic feet or 8 bushels of manure. The solution may be sprayed on the manure with a hand pump. The hellebore has no injurious effect on the manure.

Powdered borax used at the rate of 1 pound to 16 cubic feet of manure is very effective. The powder may be distributed over the manure and wet down by sprinkling with water. Care should be taken not to treat the same manure more than once. When borax is applied at the above rate there is no deleterious effects on the fertilizer value of the manure unless the manure is applied to the land in excess of 15 tons to the acre.

Foreman and Graham-Smith (1917) recommend the treatment of manure with coal-tar oil, especially creosote oil. This should be sprinkled on the heap each day after the fresh manure is added. One hundred cubic centimeters should be used for each horse per day. By such a daily increment fly breeding may be prevented. They also recommend the spraying of carcasses with a cresote solution that destroys the odors, prevents the development of maggots, and stops the putrefactive processes. This method should be of value where it is impossible to burn or bury deeply animals that have recently died. It was used with some success during the World War I when flies and putrefying bodies made conditions almost unbearable. The creosote recommended is a coal-tar creosote oil containing 14 to 18 per cent tar acids.

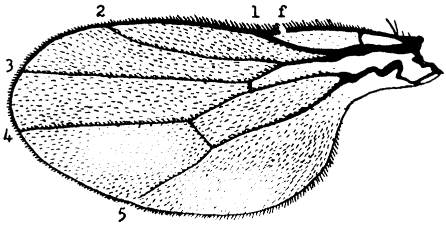
In addition to cleanliness and the treatment of manure, various types of traps for the adults (Fig. 177) and larvae are highly recommended about the milk houses and stables. Screens should be employed on the home and the milk house, and all utensils used in handling milk should be screened from flies. From the standpoint of disease it is extremely important that farmers should control flies.

Larval traps are based on the fact that the mature maggots migrate from the manure heap toward the margins or bottom. This is especially true if the manure is well packed and "heating" takes place. Under such conditions the maggots do not penetrate more than one to three inches below the surface, thus preventing excessive breeding. Several types of larval traps have been devised and are used where conditions make them desirable as at army posts and residences near which horses are stabled. The most elaborate trap in that devised by Baber (1918 and 1925). This was modified by Allmett (1926). Hutchison (1915) devised a somewhat simpler type that is said to be effective. As Baber's trap is rather expensive to construct and chiefly suitable for permanent army and cavalry posts, the reader is referred to the original publications. Hutchinson's trap is simple and easily installed. It consists of a concrete pit 4 inches deep and of varying size, depending on the amount of manure to be stored. A pit 22 feet long and 12 feet wide will serve for holding the manure from three horses for about four months. A drainage outlet should be provided at one end of the pit. This opening can be plugged when the pit is in use. The manure is not stored in the pit but is placed on a lattice framework supported on legs within the pit. The lattice tops should be about 6 inches above the top of the pit and the margins at least 1 foot from the inner margins of the concrete walls. When in use the bottom of the pit is covered with at least 1 inch of water. The horse manure is piled carefully on the top of the lattice platform each day and moistened. In this way large numbers of flies will be attracted for egg-laying purposes. The mature larvae will migrate downward or to the margins and drop into the pit where they will be drowned. If the water in the pit is kept covered with a layer of fuel oil, the maggots will be killed more quickly and at the same time mosquitoes will be kept from breeding. By this procedure the adults are attracted to the trap for oviposition, but rarely will any of the larvae succeed in reaching the adult state.

The problem of fly control is an ever-present one. Fly-control campaigns have been organized and carried on with great vigor in many parts of the world. The effects of such campaigns usually wear off in a few years and conditions gradually become as bad as ever. The "swat the fly" campaigns are usually futile for our efforts are directed away from the essential basis of fly control, the prevention of fly breeding. It is highly desirable to kill flies, but do not let such efforts obscure the fundamental necessity, if we are to reduce the fly population to any marked degree, of directing our endeavors to the bettering of sanitary conditions. The effective educational work carried out along sane and sensible lines will produce better results than short, intensive campaigns. If our health officers are adequately supported by an intelligent public opinion, they can gradually develop the desire for cleanliness of person, of home, of private and public buildings, of all operations concerned with the disposal of garbage and wastes, and of farming operations. Until we can instill into the great body of our citizens the desire for cleanliness in all things, we can hope for very little progress by the passage of drastic sanitary laws which, difficult to enforce, ofttime defeat the ends they were intended to serve.

THE FAMILY CHLOROPIDAE (OSCINIDAE)

This is a family of very small flies, rarely exceeding 3 mm. in length. The family may be recognized by the absence or great reduction of the squamae, the lack of a longitudinal suture on the second antennal segment, the subcosta vestigial, the presence of only one fracture on the costa, and the absence of the sixth longitudinal and anal veins (Fig. 178). The most important genera, from a medical standpoint, are *Hippelates* and *Siphunculina.* The latter genus contains what has been called the "eye fly" (*S. funicola* de Meyere) of India, Cey-



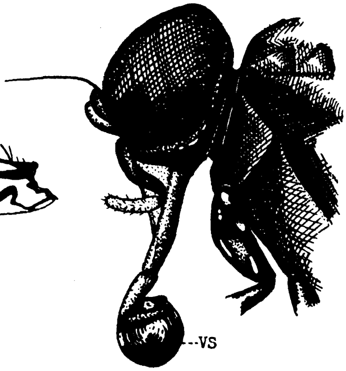


Fig. 178 (*left*). Wing of *Hippelates* sp. Note the absence of the sixth vein and only 1 fracture (f) on costa.

Fig. 179 (*right*). The eye gnat, *Hippelates pusio,* showing the "vomit spot" (VS). (Sketched from a photograph by Kumm.)

lon, Java, and other Eastern countries. Roy (1928) presents evidence that the prevalence of this fly in Assam corresponds closely to epidemics of naga sore and conjunctivitis. Though these flies are incapable of piercing the skin and taking blood, their mouth parts are so constructed (somewhat like those of the housefly) that each labellum has the tips of the six pseudotracheae upturned and sharp, so they can abraid the edges of sores and the conjunctival epithelium about the eyes or make small multiple lesions about wounds.

HIPPELATES FLIES: EYE GNATS

Species of the genus *Hippelates* have long been suspected of being involved in the transmission of pinkeye or "sore eye" in various parts of the southern United States. Herms (1928) pointed out that *Hippelates pusio* Loew (as *flavipes* Loew) was probably responsible for the epidemics of pinkeye in the Coachella Valley, California. Bengston (1933) reported similar conditions in Florida and incriminated the same species as the vector. It appears well established that this fly acts as a mechanical vector of this type of conjunctivitis in various parts of the southern United States, especially in southern California. Flies of this genus have also been regarded as playing some part in the spread of yaws.

Hippelates pusio Loew (Fig. 180) is a small (2 mm.) blackish fly with yellowish legs, the femora being usually brownish or black on the basal half. The eyes are prominent and appear yellowish in mounted specimens. Antennae are bright yellow, the last segment bearing a long, hairlike arista. The thorax is shining black, with numerous short, fine hairs arranged in rows. The wings are hyaline (Fig. 178) and are held crossed, scissorlike when at rest. Each hind tibia has a very long, thin spine near its distal end.

This fly frequently occurs in immense numbers, as in the Coachella Valley, California. Hall (1932) describes in detail its biology and habits. The adults are not attracted to lights at night but favor the bright sunlight during the day. They are attracted to wounds, pus, sebaceous material, and especially to secretions about the eyes. They swarm about in immense numbers and are very annoying. In California they are most abundant during the spring (March to May) and autumn (August to October), though they breed throughout the year where conditions are favorable.

The females lay their minute, curved, fluted eggs in loose soil heavily charged with organic material. They also breed in human and other animal excrement, especially when mixed loosely with soil. The adults are not long-lived but the life cycle from egg to adult is short, varying from two to four weeks (longer in cool weather), so that a dense population of adults is maintained during favorable breeding conditions. The larva is legless, short (3.3 mm.), cylindrical, white, and possesses a single mouth hook with which it feeds and propels itself. The larval period varies from a few days to much longer in cool weather. Pupation takes place in the medium in which the larvae live.

Hippelates pallipes Loew is an abundant species in Jamaica, throughout most of the West Indies, and in other parts of tropical America. Kumm (1935, 1936) has studied this species extensively in Jamaica but did not succeed in finding its natural breeding places. He reared it under artificial conditions, and its life cycle is quite similar to that of *H. pusio*. As this is the most abundant *Hippelates* species in Jamaica, studies were confined largely to its importance as a vector of yaws. Kumm *et al.* (1935) records this fly as feeding in enormous numbers on yaws lesions, especially those on the lower extremities. They found large numbers of the spirochete, *Treponema pertenue,* in the esophageal diverticulum, and these remain alive for at least seven hours and some of them may be regurgitated in the vomit spot (Fig. 179) when they feed on a susceptible person. Spirochetes that pass into the digestive tract are all digested. Any transmission of yaws is purely mechanical, no developmental cycle occurring in the fly.

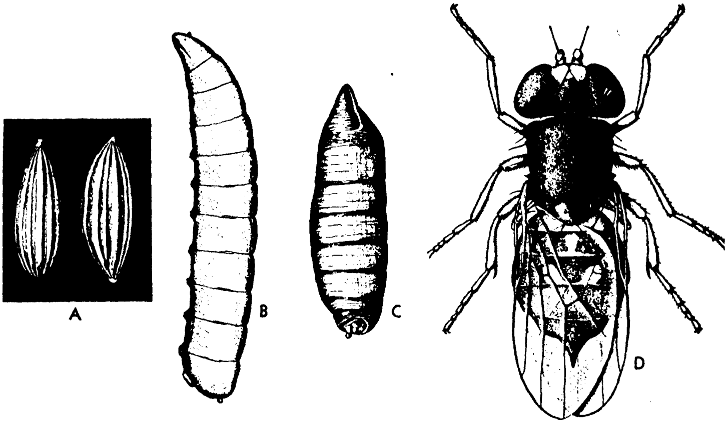


Fig. 180. The eye gnat, *Hippelates pusio.* (*A*) The egg. (*B*) The larva. (*C*) The puparium. (*D*) The adult. (All after Hall.)

CONTROL: Various methods have been tried to control these pests but without great success. Traps, general sanitation methods, and improved agricultural practices have given some relief. When more is known of the larval breeding places, it may be possible to clean up bad areas by the use of DDT or some of the newer insecticides by directly treating the soil. The use of repellents employed against mosquitoes and blackflies may be of some value.

IDENTIFICATION OF OUR COMMON MUSCID FLIES[3]

Flies About the Home; Flies That Cause Myiasis; Flies That Are Bloodsucking in Habit

Hypopleural bristles absent 1
Hypopleural bristles present (Fig. 85) 11
1. Sixth vein very short; seventh vein tends to curve under the sixth; fourth vein straight .... *Fannia* (*Homalomyia*)
Sixth vein fairly long; seventh vein straight; fourth vein bowed or angled near its distal end (Fig. 172) 2
2. Proboscis long, directed forward, and fitted for piercing 3
Proboscis not elongate; the labella fleshy and not adapted for piercing .. 5
3. Rays of arista plumose (Fig. 168). (African species) .... *Glossina*
Rays of arista simple, not plumose 4
4. Palpi much shorter than the proboscis .... *Stomoxys*
Palpi nearly as long as the proboscis .... *Haematobia*
5. Arista bare .... *Synthesiomyia*
Arista pectinate (plumose on the upper side) .... *Hemichlora*
Arista plumose 6
6. Large species (about the size of worker bumblebee) with conspicuous black and yellow pile .... *Hypodermodes*
Smaller species (about the size of the housefly) without dense black and yellow pile 7
7. Color metallic bluish black or green; stripes evident on anterior margin of thorax 8
Color opaque gray or black 9
8. Middle tibia with a prominent bristle on its surface beyond the middle .... *Pyrellia*
Middle tibia without such a prominent bristle .... *Morellia*
9. The last section of fourth vein distinctly angled (Fig. 172); sternopleural bristles 1:2; eyes bare .... *Musca*
The last section of the fourth vein gently bowed (Fig. 192) 10

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[3] For the identification of flies to families consult the key on pages 228–231.

10. Eyes hairy; sternopleural bristles 2:2 .... *Myiospila*
    Eyes bare; sternopleural bristles 1:2 .... *Muscina*
11. Body color opaque gray or black, never shining metallic; arista bare or pubescent 12
    Metallic blue or blue-green species, or the abdomen, at least, shining metallic bluish black 13
12. Thorax with deciduous yellow, curly pile among the macrochaetae against a shining black background .... *Pollenia rudis*
    Thorax without deciduous yellow, curly pile but with four distinct grayish lines .... *Wohlfahrtia vigil*
13. Basal section of first vein (the part preceding the humeral cross vein) ciliated (bearing fine hairs) 14
    Basal section of first vein bare 17
14. Bucca and face, yellow with yellow pile; one posthumeral bristle .... (Formerly *Chrysomya* or *Cochliomyia*) *Callitroga*
    Bucca black with black hairs; usually two posthumeral bristles 15
15. Squamae white; anterior acrostichals well distinguished from the surrounding hairs 16
    Squamae darkened; anterior acrostichals not distinct from the surrounding hairs; prothoracic spiracle black .... *Protophormia*
16. Four intra-alar bristles; six or more marginal scutellar bristles; mesothoracic spiracle dark orange to black .... *Protocalliphora*
    Two intra-alar bristles; four marginal scutellar bristles; mesothoracic spiracle distinctly light-orange-colored .... *Phormia*
17. Upper surface of lower squamae (calypter) bare (Fig. 85) ...... *Lucilia*
    Upper surface of lower squamae distinctly pilose 18
18. Two bristles near middle on exterior surface of front tibia; one sublateral bristle (posthumeral) .... (*Cynomyia*) *Cynomyopsis*
    One, rarely two, bristles near middle on exterior surface of front tibia; three sublateral bristles .... *Calliphora*

SPECIES NOTES

Fannia: Two species are not infrequently the cause of intestinal myiasis and are commonly found in houses. They are *F. canicularis* and *F. scalaris.*

Stomoxys: There is only one species in the United States, *S. calcitrans.* Other species occur in different parts of the world.

Musca: Only one common species, *M. domestica.* Other species occur in the Orient, the Ethiopian region, and Europe.

Muscina: There are two common species in America, though a third (*pascuorum*) has recently been introduced:

1. Legs entirely black; palpi reddish yellow .... *M. pascuorum*
   Legs not entirely black, usually some yellow present; if black, palpi black 2
2. Palpi black; tibiae usually mostly black though a yellowish tinge may be present .... *M. assimilis*
   Palpi yellow; tibiae and distal portion of femora yellow ...... *M. stabulans*

Pollenia: Only one common species, *P. rudis.*

Calliphora: We have three common species:

1. Three intra-alar bristles .... *C.* (*viridescens*) *livida* [4]
2. Two intra-alar bristles ....
   B. Bucca black; beard reddish .... *C. vomitoria*
   BB. Bucca brownish or reddish; beard black *C.* (*erythrocephala*) *vicina* [5]

Lucilia: We have three common species:

1. Two postacrostichals (Fig. 85) .... *L. illustris*
2. Three postacrostichals ....
   B. Palpi black .... *L. silvarum* [6]
   BB. Palpi yellow .... *L. sericata* [7]

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[4] According to Hall (1948) *viridescens* is not recognizable and he describes our American species as *C. livida* n. sp.

[5] The species name *erythrocephala* is preoccupied and Hall (1948) adopts *vicina* R.D. (1830).

[6] Hall (1948) places this species in the genus *Bufolucilia.*

[7] The same author assigns this species to the genus *Phaenicia.* These last two changes do not seem necessary. The splitting of the genus *Lucilia* is unfortunate.

[8] The literature on the housefly and related species is so extensive that only a comparatively few references can be given here.

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CHAPTER XVII

Myiasis of Man and Allied Conditions

THE infection of man by insects has been known from ancient times. Though there is a number of scattered references from which almost definite identification of the invading insect can be determined, it was not till early in the nineteenth century that observations became somewhat specific. Hope (1840) brought together all the more definite references to insect larvae invading man and evolved a terminology that is in use at the present time. The invasion of man and animals by dipterous larvae he termed myiasis; by coleopterous larvae, canthariasis; by lepidopterous larvae, scoleciasis (a term first used by Kirby and Spence in 1815 to include all infestations of man and animals by insects and their larvae). Hope records 63 cases of myiasis, 35 of canthariasis, and 7 of scoleciasis. Since that time there have been almost innumerable references to insect invasions of man and animals, but most of them are brief; no specific determinations are given or are possible. Even at the present time our knowledge of these infections is rather meager. The following account is largely restricted to conditions found in the Americas.

The term myiasis is restricted to the infections of man and animals caused by the invasion of dipterous larvae. The various types of myiasis are usually designated by the localization of the invading larvae: cutaneous or dermal (in the skin or subcutaneous tissues), gastric (in the stomach), intestinal (in the intestines), urogenital (in the urogenital tract), aural (in the ear), nasal or rhinal (in the nose), ocular (in the eye), etc. From the standpoint of the entomologist, this classification is rather unsatisfactory, but it meets the needs of the pathologist and the physician. Patton (1921) has proposed another grouping based on the habits of the flies and, though not a zoological arrangement, it gives us a much better conception of the relation of these flies to their hosts. This arrangement is briefly outlined at the end of the chapter. For our purposes it will be more satisfactory to discuss these myiasis-producing flies according to the families they represent. (For a classification of flies see pp. 486–488). ?

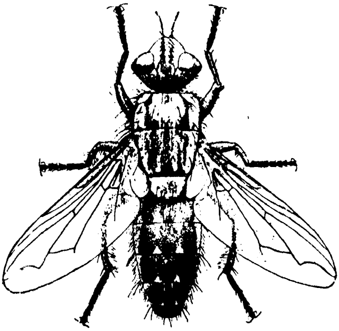
THE FAMILY SARCOPHAGIDAE (Metopiidae)

The family Sarcophagidae (flesh flies) contains comparatively few genera, but the species are numerous and very abundant. These flies are rather large (Fig. 85) and the coloration is generally quite uniform. As a group they are dull-colored, the thorax striped longitudinally with gray and the abdomen marmorate. The arista is plumose or strongly pubescent to the middle, bare beyond (this is one of the most distinctive characters of the family). The abdomen is not strongly bristled and the bristles are restricted to the apical portion. The larvae are typically muscoidean (Fig. 173) but may be distinguished by the presence of a girdle of minute spines on the abdominal segments. The mouth hooks are well developed, curved, and provide good weapons for the tearing of tissues. The larvae are amphipneustic. The posterior stigmal plates (Fig. 182) are situated in a deep cavity; the slits are three in number for each spiracle and are arranged nearly vertical and parallel.

The adults are everywhere abundant, especially about decaying vegetation, fruit, excrement, decomposing animal matter, and similar conditions. As far as is known all the species are larviparous, depositing, not eggs, but living larvae. The larval habits are extremely varied: some are parasitic on warm-blooded animals, on insects (Orthoptera), on snails, etc.; many are scavengers; and others occur in wounds, sores, ulcers, or cavities from which foul-smelling material is being discharged. Both the adults and larvae are very difficult to identify. As yet it is scarcely more than possible to place the larvae in the family, though some generic distinctions have been attempted (Root, 1923). The adults can only be determined by experts, though the work of Aldrich (1916) lessens the labors of beginners. Wherever the larvae of the flesh flies are found, every effort should be made to rear the adult so that positive records may be obtained. The following notes are mainly restricted to American species.

THE GENUS *WOHLFAHRTIA*

Wohlfahrtia vigil Walker is a large, grayish fly (Fig. 181) measuring 7.5 to 14 mm. in length. It is widely distributed in eastern North America. Walker (1920, 1922) first recorded its attacking man; he reared the adults from larvae obtained from an infection of a young child at Toronto, Ontario. The lesions occurred on the left side of the neck under the jaw (Fig. 183). On the removal of the maggots the wounds healed rapidly. Unlike other myiasis-producing Sarcophagidae, this species attacks the healthy skin, not entering through one of the nautral orifices as the nose, ear, or open sores. Walker (1931) gives a résumé of eight cases reported from man. Felt (1924) reports what he believes is a case of ocular infection. Several first-stage larvae were removed from the conjunctiva of a man in Cattaraugus County, New York. The larvae were found in a small cyst. Sanders (1928) records a case of infection in a child three months old. The larvae were present in superficial pustules on the neck. Two additional cases can be reported from New York state. The first was in a young child at Utica. The attending physician removed several maggots from pustules on the neck. The larvae were sent to the writer and definitely identified. The second case occurred in young puppies about four weeks old. Four mature larvae were removed from deep cutaneous lesions and identified by the writer. Shannon (1923) records the rearing of this species at Ithaca from larvae found deeply embedded in the shoulder muscles of rabbits. Gerston *et al.* (1933) reported two cases in babies in North Dakota. At the present time this species has been recorded from children, rabbits, cats, foxes, mink, ferrets, and puppies. Undoubtedly it has many more hosts. Ford (1936) gives an extended account of this species. The adults are not attracted to exposed meat nor do they oviposit on it. They were found in nature in warm areas as along railroad tracks (or on hot sidewalks, by the writer) and fed apparently on the nectar of such flowers as wild caraway, milkweed, sweet clover, early goldenrod, and probably other plants. The females, when ready to oviposit, dart suddenly at their host, usually alighting on the head beside the eyes or mouth, and deposit a number



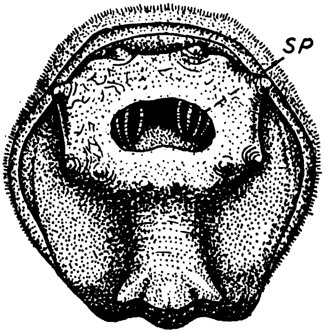
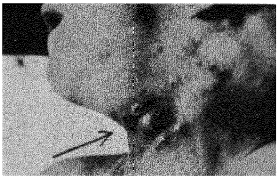


Fig. 181 (left). Wohlfahrtia vigil. (After Walker, *Journal of Parasitology.*)

Fig. 182 (right). Posterior spiracles of larva of *Wohlfahrtia vigil.* Note their location in a deep pit at posterior of body (SP).

of larvae. The larvae immediately penetrate the tenderest skin and grow rapidly, producing a distinctive lesion. The larval period varies from 7 to 9 or more days and the pupal period is about 10 to 12 days. The females are ready to larviposit in about 13 to 17 days after emergence.

The mature larva [1] measures 16 to 18 mm. in length. The cephalopharyngeal apparatus (Fig. 184) is very characteristic and is fully explained in the figure. One of the most distinguishing characteristics of the larva is a band, more or less interrupted, of minute spinules present on each of the body segments. These bands of spinules are more pronounced in the first and second larval stages. The posterior spiracles are located in a deep pit (Fig. 182). Each spiracle has three slits arranged as shown in Fig. 194 *3;* the peritreme is well developed but does not completely surround the spiracle. The button is not well developed. Each anterior spiracle consists of 9 to 10 stout, fingerlike processes.



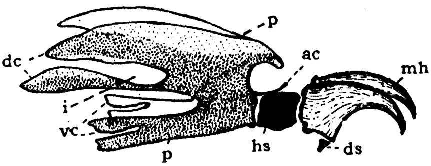


Fig. 183 (*left*). Male infant infected with larvae of *Wohlfahrtia vigil.* The arrow points to the seat of infection. (After Walker, *Journal of Parasitology.*)

Fig. 184 (*right*). Cephalopharyngeal skeleton of the mature larva of *Wohlfahrtia vigil.* ac, rodlike process of pharyngeal sclerite; dc, dorsal cornua; ds, dental sclerite; hs, hypostomal sclerite; i, incision of dorsal cornua; mh, mouth hooks; p, pharyngeal sclerite; vc, ventral cornua.

Wohlfahrtia opaca Coq. (*meigenii* of authors) is a closely allied species found in the western United States but nothing is known of its biology.

Wohlfahrtia magnifica Schiner is an Old World species widely distributed in southern Europe, Asia, and Africa. It deposits living larvae in all sorts of wounds, sores, diseased eyes, nose, ear, vagina, soiled wool, etc., and is a serious pest of domestic animals as well as man. In its habits it closely resembles the screwworm (*Callitroga americana*) of America.

THE GENUS *SARCOPHAGA*

Sarcophaga haemorrhoidalis Fall, is a large grayish fly, 10 to 14 mm. in length. It has a wide distribution in America, Europe, Africa, and Asia. Aldrich

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[1] The mature larvae of myiasis-producing flies can generally be recognized by the cephalopharyngeal structure and the posterior spiracles (see figures).

(1916) reports that a Mr. J. B. Gill of Monticello, Florida, evacuated numbers of nearly mature larvae in his stools; from these eight adults were reared. He also records the rearing of adults by Haseman from larvae passed in human feces. The larvae came from a young girl, the members of whose family had been troubled for several years by intestinal myiasis. It is believed that most of the records of *Sarcophaga* species causing intestinal myiasis refer to this fly. The species normally breeds in carrion, decomposing animal matter, etc. In the cases of human infection the females probably deposit their larvae on soiled food or other substances eaten by man.

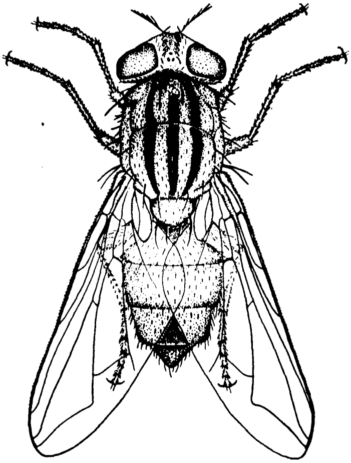
OTHER SARCOPHAGID INFECTIONS: Higgins (1890) records large numbers of sarcophagid larvae vomited by a child only 18 months old. Riley (1906) reports the infestation of a tumor on the back of an elderly woman by 10 or 12 maggots. Patton (1923) figures a cutaneous myiasis of the cheek caused by the larvae of *Sarcophaga fuscicauda.* Keilin (1924) reports a case of intestinal myiasis by a sarcophagine fly. Wohl (1913) gives an account of a young man relieved after the expulsion of sarcophagid larvae; these were reared and identified as *Sarcophaga sarraceniae* (?) Riley.

THE FAMILY CALLIPHORIDAE

In this family the species are usually quite large and the body, especially the abdomen, is metallic blue, green, or varying shades of these colors. Here belong the blowflies, the bluebottle flies, the green-bottle flies, and some others. Many of the species are very serious pests to domestic and game animals and some occasionally attack man. In general their larvae develop in fresh or decaying flesh, destroying the carcasses of dead animals (scavengers); some consistently are found in wounds and sores of all kinds; other attack the young of nesting birds (bloodsucking larvae); some breed in dung; and one species, *Pollenia rudis,* (the cluster fly) is parasitic on species of earthworms. Only the more important species are treated here.

THE GENUS *CALLITROGA*

Callitroga americana (Cushing and Patton), the screwworm fly, is the most important American species. The adult varies from 8 to 10 mm. in length and is metallic green in color, with three distinct longitudinal dark stripes on the thorax (Fig. 185); the head is bright yellow and the eyes reddish yellow. It is widely distributed in the Americas, extending from the southern part of the United States southward to southern Brazil and northern Chile (Hall, 1948). In the United States it is most prevalent and injurious in the South and Southwest. Its range frequently extends northward to central California in the West and northern Iowa and Indiana in the East. The species cannot survive temperatures below 20° F. for the adults or 15° F. for larvae or pupae. It breeds throughout the year in the extreme southern part of the United States. The adults do not hibernate. It is also a serious pest in parts of Central America, Panama, and South America. This species was confused with *Callitroga macellaria* (Fabr.) until Cushing and Patton (1933) definitely demonstrated that the true "screwworm" fly was an undescribed species. As a result, most of the references in our literature refer either to one or the other or a mixture of the two. The following account is based on the detailed studies made of this species by various members of the United States Bureau of Entomology.



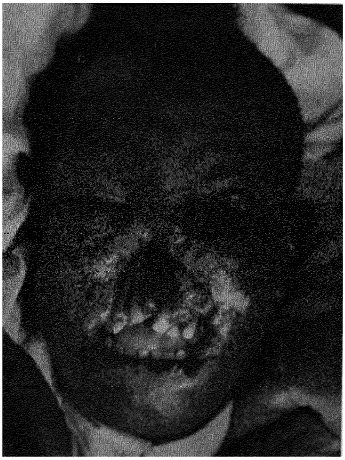


Fig. 185 (*left*). Adult female of *Callitroga americana,* the American screwworm fly. *Fig. 186* (*right*). Effects of an attack of the American screwworm fly on a patient. (Courtesy of U.S. Department of Agriculture, Bureau of Entomology.)

BIOLOGY AND HABITS: This species is an obligatory parasite, the females ovipositing only in fresh wounds of man and other animals. It is not saprophagous. It probably is the chief cause of myiasis throughout its range. The adults are said not to be active but remain resting, though they can range long distances, 11 miles as reported by Parrish (1937). They have been observed in nature feeding upon wounds, fresh meat, and fresh manure. Brody (1939) fed the flies on a wide variety of foods. When oranges, grapefruit, tomatoes, or cantaloupes were supplied daily, the flies survived the preoviposition period (9 days) and laid viable eggs. On meat or its products eggs were never obtained. The gravid females appear to select wounds 2 to 10 days old. Each female lays from 10 to nearly 400 eggs in a shinglelike mass tightly glued to the edge or surface of the wound, near the dry scab, or on dried blood clots. The eggs hatch in from 11 to about 21 hours and the young larvae immediately penetrate and feed on the tissues of the wound. As they penetrate deeply the posterior spiracles are directed upward to keep in contact with the air. Growth is rapid. The larvae feed gregariously and produce a deep, pocketlike injury (Fig. 186). The larvae mature in from 4 to about 8 days depending on conditions of the wound. Dropping to the ground they pupate in the soil. The pupal period varies from 7 days in the hot summer to 54 days in winter (Texas).

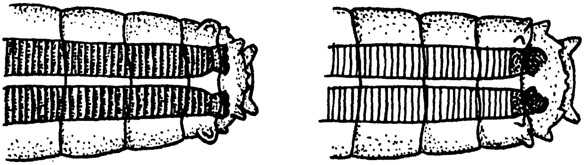


Fig. 187. Left: Posterior end of larva of *Callitroga americana. Right:* Same of *Callitroga macellaria,* the false screwworm fly. Note the appearance of the tracheae, heavy and dark in *C. americana.*

The mature larva is typically muscoid in appearance. It is nearly 17 mm. in length and each segment is banded with rather stout spines. The tracheal trunks leading from the posterior spiracles are pigmented through the last three or four segments (Fig. 187). The pigmented tracheal trunks and the presence of spines on the dorsal and lateral margins of the two segments next to the last one will distinguish the larva of *C. americana* from that of *C. macellaria.*

RELATION TO DISEASE: As this species has been confused for a long time with *C. macellaria* (Fabr.), the numerous references to myiasis of man and other animals are difficult to interpret. However, the data all indicate that the latter species is only a secondary invader and is primarily a scavenger. All primary infestations of nonputrid wounds are by *C. americana* (Cushing and Patton). This fly may deposit its eggs on any wound, however small, such as a scratch or injured toenail, and numerous cases of human infection by this species have been recorded since the status of this species was recognized (1933). It is a very dangerous pest of cattle, sheep, goats, and other animals. In 1934 during a severe outbreak of this species in the southeastern United States over 1,300,000 cases were reported, while in 1935, 1,200,000 cases were recognized in Texas alone.

The attacks were so severe that thousands of animals died, and James (1947) reports a mortality rate of nearly 20 per cent in uncontrolled cases. The wound made by these larvae is deep-seated (Fig. 186), and when heavy infection of the nasal and frontal regions, of the eyes, ears, and mouth, occurs, death usually results if it is not treated promptly. The navel and vaginal regions are often invaded by the maggots and serious conditions ensue (Fig. 188).

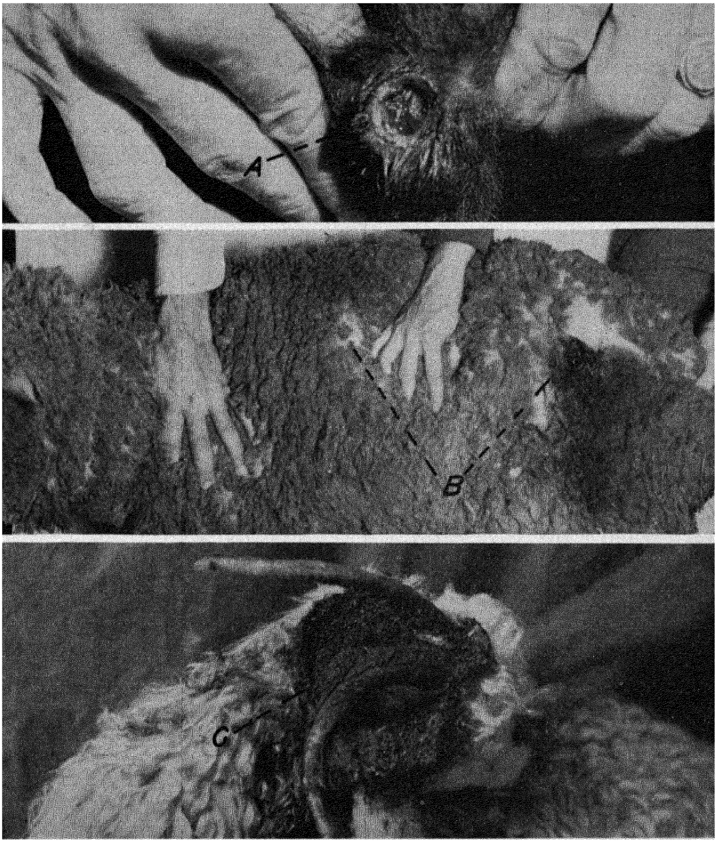


Fig. 188. Callitroga americana infestation. (*A*) Of the navel of a young calf. (*B*) Of a sheep. (*C*) Of head of goat, a severe case. (Courtesy of the U.S. Bureau of Entomology and Plant Quarantine.)

During these outbreaks Dove (1937) listed 55 human cases for 1935 (and estimated over 100 cases) but only 8 cases for 1936. This great reduction in human infestation was undoubtedly due to the excellent results obtained by the development of control measures and the widespread use of Smear 62, developed by the United States Bureau of Entomology. In the human cases infestation occurred in the nose, eyes, vagina, sarcomas, small wounds, scratches, bruises, blood clots, and similar places. There were no deaths where medical treatment was obtained, but several deaths occurred in untreated cases. Nasal infestations are usually extremely painful, the patient frequently becoming delirious. In one case of nasal infection in Texas Dove reports the physician removing 385 larvae during a nine-day period.

CONTROL: The most effective control methods involve the prevention of wounds in animals due to barbed wire, fighting, dehorning, or other agencies. If wounds become infested the use of Smear 62[2] is most effective. It is prepared as follows (United States Bureau of Entomology):

1. Diphenylamine (Tech. grade)	3½ parts by weight
2. Benzol (P.P.)	3½ " " "
3. Turkey red oil (pH 10 or neutral)	1 part " "
4. Lamp black	2 parts " "

Dissolve 1 in 2 and allow to stand for about a day. Add 3 and mix thoroughly; 4 is added gradually and the mixture stirred till it reaches the consistency of molasses. This mixture should be stored in a tight container in a cool place. As benzol is highly inflammable, no fire or other hazard such as lighted cigarettes or cigars should be near when making or using the mixture. If it becomes too thick the addition of benzol will bring it back to the necessary consistency. On animals apply with a small paintbrush (about 1-inch size). Clean each wound and apply carefully. Avoid getting it into the eyes. This treatment should be repeated every few days till the wounds heal.

In human infestations the physician should be consulted immediately as delay may be serious. The maggots develop so rapidly that failure to obtain treatment may result in serious complications. When these flies are abundant certain precautions should be observed. Avoid sleeping in exposed places, such as porches and open rooms, or out of doors unless nets are employed. Small wounds, exudates from the eyes, nostrils, or other regions, exposed blood clots, or abrasions should be carefully treated so that healing may be prompt. The maggots cannot penetrate the unbroken human skin though they can that of rabbits and guinea pigs.

Callitroga macellaria (Fabr.) is usually referred to as the secondary screwworm fly. The adult closely resembles the primary screwworm fly in coloration. It is more bluish metallic but otherwise similarly colored. About the only obvious difference is that the short hairs of the parafrontals are white to yellowish, whereas in *C. americana* these hairs on the upper half are black (to base of antennae) and golden on the lower portion. The most distinguishing characters are found in the male genitalia. The length is 6 to 9 mm.

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[2] At the present time several other effective smears are on the market.

This species is widely distributed in the Nearctic and Neotropical regions, extending from central Canada south through the United States, Mexico, Central America, the West Indies, and South America to Patagonia.

The adults are active fliers and swarm about carrion, especially in warm, humid weather. They are wide-ranging as Bishop and Laake (1921) report migrations of 8 miles in 24 hours, 10 miles in less than 48 hours, with a maximum of over 15 miles. Though they primarily lay their eggs on carrion, yet they oviposit about festering wounds or wounds infested with *C. americana* where the larvae feed on the necrotic tissues and wastes. On carrion the females deposit thousands of eggs, sometimes in immense masses. The eggs hatch in from 6 hours to much longer in cool weather. Growth is rapid, the larvae becoming mature in 6 to 20 days. The larvae enter the soil to pupate and the adults emerge in 3 or more days. The entire life cycle from egg to adult varies from 6 to 39 days (Bishopp, 1915). After emergence, mating takes place and the females begin laying eggs in 3 to 18 days. Each female may lay several batches of eggs, but her life is short—only two to six weeks. In southern Texas Bishopp (1915) reports from 10 to 14 broods annually. In the North breeding ceases at temperatures below 40° F., in fact Bishopp states that 50° to 60° F. is the minimum temperature for fly activity.

The larva closely resembles that of *C. americana* but can be recognized by the absence of dorsal and lateral spines on the two abdominal segments preceding the last one and the lack of pigmentation on the tracheal trunks (Fig. 187).

Though this species attacks carrion primarily, it will oviposit on sheep with wool dirtied by urine or fecal wastes, on festering sores, or on any animal with contaminated wounds. Though it has frequently been reported from man, it is believed most of such infestations were due to *C. americana*.

THE GENUS *CHRYSOMYA*

Chrysomya bezziana is a species closely related to our screwworm fly. It is a common fly of Africa, Asia, and the Philippine Islands. Though it mainly infests wounds, sores, ulcers, etc., of animals, Patton reports it as a serious invader of man (in India) and records the larvae from all sorts of wounds—sores, ulcers, the nose, eye, ear, vagina, and gums. There are a few human records from Africa and none from the Philippines. In Africa Cuthbertson (1933) states that "next to the Tsetse fly (*G. morsitans*) this blowfly is the most important pest of cattle, sheep, horses, dogs and other domestic animals in Rhodesia." He notes that the complete life cycle occupies 14 to 18 days and that there are eight generations a year. The females are very prolific, each female laying from 500 to 600 eggs. The spread of this fly to the Americas would add another serious pest of our domestic animals and probably also man.

Other species of *Chrysomya* that attack domestic animals and occasionally man are *C. marginalis* (Wied.), common in Africa (mainly a scavenger); *C. albiceps* (Wied.), widespread in Europe, the Middle East, India, and Africa (one of the important sheep maggots in South Africa); *C. chloropyga* (Wied.), important sheep pest in South Africa; and *C. rufifacies* (Macq.), a pest of sheep in Australia. Some of these have been reported from man.

THE GENUS *CALLIPHORA*

The genus *Calliphora* (Fig. 189) contains a number of species of which three are our common blowflies or bluebottle flies—*C. vomitoria* (Linn.), *C. vicina* R.-D. (*erythrocephala* Meig.), and *C. livida* Hall (= *viridescens* R.-D.) (See table for identification of these three flies on pp. 486–488). The first two species are the most common and abundant. The three species resemble each other very closely in size, coloring, and habits. Each varies from 7 to 12 mm. in length, with a wing expanse of about 25 mm. The eyes are red, the thorax is bluish gray with indistinct, longitudinal, darker blue stripes, and the abdomen is somewhat paler blue with whitish pubescence on the anterior half of each segment. They are stout, active flies and produce a rather characteristic loud buzzing sound during flight. They frequent places where meat or decaying animal and vegetable matter are exposed and are always abundant about slaughter houses, piggeries, and unclean places of all kinds. They oviposit on exposed flesh. The developmental cycle is very rapid. The eggs hatch in from 8 to 24 hours, and the larval growth is completed in from 4 to 9 days; pupation takes place in the soil and the adults emerge in from 10 to 17 days. The entire life cycle requires from two to four weeks. *C. vicina* and *C. vomitoria* are Holarctic in distribution; *C. livida,* Nearctic. The larvae can usually be identified by the cephalopharyngeal structure and posterior spiracles (Figs. 190,194,195).

Though development normally takes place on dead flesh, the flies frequently oviposit on wounds, sores, ulcers, or other festering places of animals and, rarely, man. Courtis (1927) removed three nearly mature larvae from a pus pocket in the left lachrymal sac of a patient. These larvae pupated and the adults proved to be *C. vomitoria*. Oronato (1922) reports a long series of infestations by various species of muscoidean flies in Tripoli. *Calliphora vicina* R.-D. (*erythrocephala*) is recorded from two human cases, and numerous infestations of various animals by different species are listed. Harvey (1934) lists the above species from a human case in England. There are also many records of the larvae of these flies causing intestinal and, occasionally, nasal myiasis.

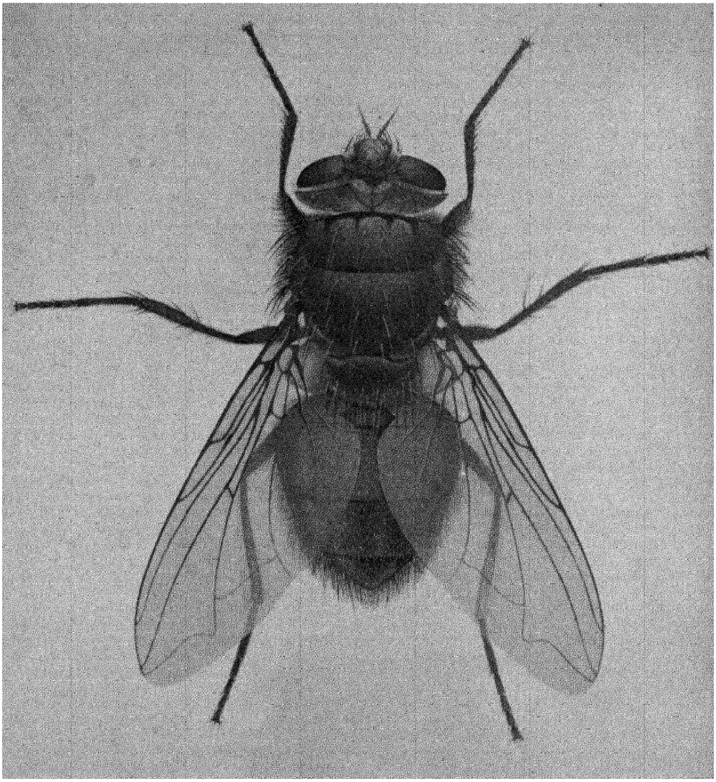


Fig. 189. The bluebottle fly, *Calliphora vomitoria,* enlarged. (Courtesy Department of Agriculture, Division of Entomology, Canada.)

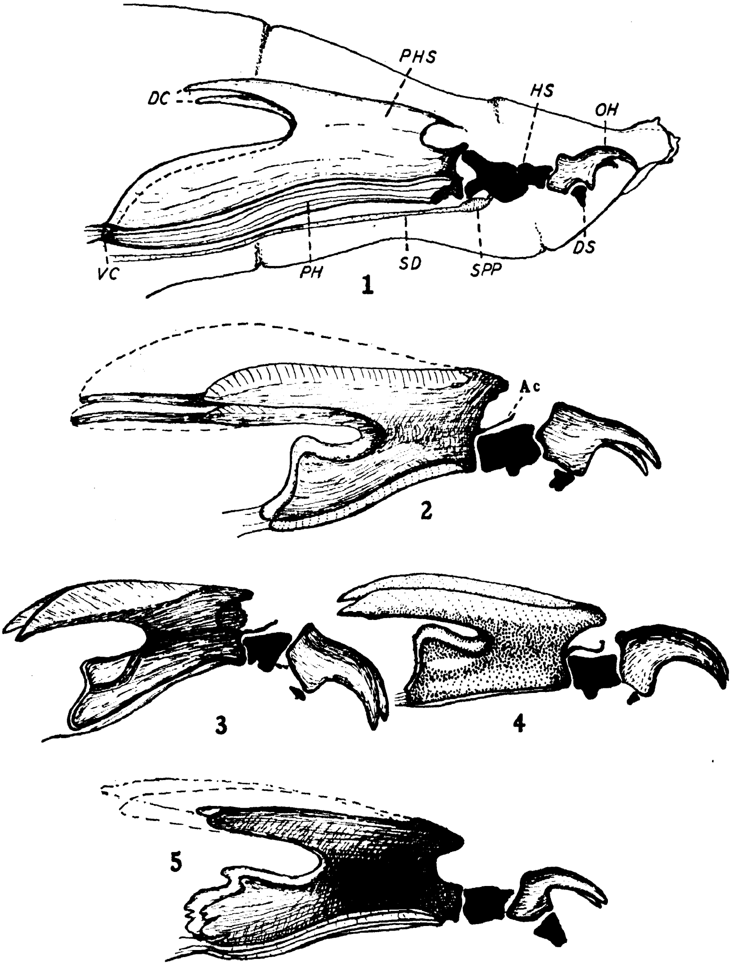


Fig. 190. Cephalopharyngeal structures of mature larvae. (*1*) *Stomoxys calcitrans.* (*2*) *Phormia regina.* (*3*) *Callitroga macellaria.* (*4*) *Lucilia sericata.* (*5*) *Muscina stabulans.* Ac, rodlike prolongation of pharyngeal sclerite; DC, dorsal cornua; DS, dental sclerite; HS, hypostomal sclerite; OH, oral or mouth hooks; PH, pharynx; PHS, pharyngeal sclerite; SD, salivary duct; SPP, salivary pump; VC, ventral cornua. (All drawn to same scale.)

THE GENUS *LUCILIA*

The green-bottle flies. This genus contains a considerable number of species about which very little is known. Unfortunately the genus has been split into a number of genera of doubtful validity. At least the following species are of some importance: *L. caesar* (Linn.), *L. sericata* Meig. (placed by some in *Phaenicia*), *L. illustris* (Meig.), and *L. cuprina* (Wied.). *Lucilia* (*Bufolucilia*) *silvarum* (Meig.) is a known parasite of toads in Europe and possibly in North America. *L. caesar* of American authors is regarded now as *L. illustris* (Meig.), and all our references are to this species since *L. caesar* is believed not to occur in North America. In America *L. illustris* is primarily a carrion feeder and is the most common green-bottle fly on freshly exposed meat or about recently killed animals. Kingscote (1932) reports it as causing myiasis in foxes in Canada, and James (1947) lists two human cases. *Lucilia* (*Phaenicia*) *sericata* (Meig.) is widely distributed in North America, Mexico, Central America, parts of South America, Europe, Asia, Africa, Australia, and many islands. It is the chief species causing myiasis in sheep in the United States, the British Isles, and South Africa; it is common in New Zealand, and it is reported from Australia. The species is mostly a breeder in carrion but causes "sheep-strike" in soiled wool, festering wounds, or sores. The females deposit their eggs in masses in such places, and the larvae feed on the diseased tissues, frequently causing severe injury. The life cycle is short—egg to adult in from 9 to 14 days. Many generations occur each season, especially in the warmer parts of its range. Human cases of myiasis by this species have been reported but these must be regarded as doubtful. This is the species formerly used extensively by Baer (1931) and others for the clearing of deep-seated wounds after surgical operations. It is probably not used now because of the discovery of better treatments. *L. caesar* (Linn.) is a Palearctic species and has been reported from other areas but these were probably mistaken identifications (probable species *L. illustris*). Its importance as a cause of myiasis cannot be stated as the correct identification of such infestations is questionable. *L.* (*Phaenicia*) *cuprina* (Wied.) is distributed throughout parts of the Ethiopian, Oriental, and Australian regions and over many islands in the Indian and Pacific oceans. In Australia this species is the principal cause of "sheep-strike" and severe losses to sheep owners are reported. Though reported from North America, Hall (1948) regards our species as distinct (*L. pallescens*). Human cases are said to occur but identifications are doubtful. The species *L. sericata, L. cuprina,* and *L. pallescens* are almost identical and it is doubtful if they are good and distinct species. The change of habit from carrion feeding to attacking festering wounds or soiled wool would not appear to be of much importance where the latter conditions are more common than dead carcasses.

OTHER GENERA

Phormia regina (Meig.), known as the "black blowfly" (Fig. 191), is a common and widely distributed species in North America, Europe, parts of Asia, Australia, and some islands in the Pacific Ocean. It is known to oviposit in old suppurating sores, particularly in sheep and goats. It is primarily a carrion feeder and is very abundant where dead carcasses lie exposed. The life cycle from egg to adult varies from 10 to 25 days. There are a few records of its invading human tissues. Stewart (1929) reports an interesting case of a woman suffering from scalp sores with heavy pus exudate. After admission to the hospital and preliminary treatment, numerous dipterous maggots were observed crawling out of the sores. The maggots were very numerous, particularly back of the ears. The larvae were reared and a definite record of this species infesting man established.

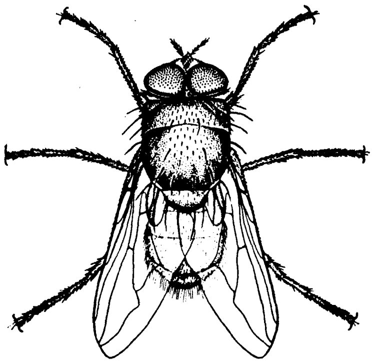


Fig. 191. Phormia regina. Female.

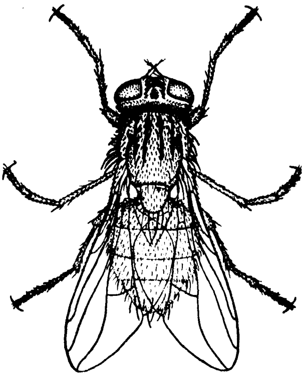


Fig. 192. Muscina stabulans. Female.

Cordylobia anthropophaga Grünberg, the tumbu fly, is widely distributed in tropical Africa, south to the Transvaal and Natal. Blacklock and Thompson (1923) have rather fully elucidated the bionomics of this species. The females oviposit in sand contaminated with fecal wastes. The female digs a small cavity for the placement of her eggs and lays, usually in two batches, some 300 to 400 eggs. At 37° C. the eggs hatch in from 24 to 48 hours; at ordinary room temperature they hatch in three days. The young larvae are stimulated to activity by heat, pressure, or movement and come to the surface to infest their hosts. They attack and penetrate the skin, completing their larval development in about 9 or 10 days. Leaving their hosts the larvae pupate in the soil. The pupal period occupies from 22 to 24 days. The principal hosts are rats and dogs; the feet of children are frequently severely infested.

Auchmeromyia luteola (Fabr.), the "Congo floor maggot," is a common species in tropical Africa. The females lay their eggs in the soiled dirt floors of the native huts. The larvae are bloodsuckers, attacking humans to obtain food and usually feeding at night. After feeding they bury themselves in the soil and come out again when hungry.

The cluster fly, *Pollenia rudis* (Fabr.), should be mentioned here not because it causes myiasis but because it is a veritable pest in our homes. The species is parasitic on several species of earthworms and there are two or three generations a year. In the cold days of autumn the adults seek shelter in buildings, and attics are frequently found swarming with them, not hundreds but thousands, and they leave behind them their filth and many dead bodies. Here they pass the winter in the North, and these large, cumbersome flies (easily recognized by the abundance of short, golden-yellow, curly pile among the hairs of the thorax and by their size—they are larger than the housefly) come out from time to time and fly with a buzzing sound through the rooms. The author has seen homes, hospitals, and other buildings just swarming with them despite the owners' efforts to prevent their entrance. They may easily be eliminated by spraying attics or other resting places with a 5 per cent DDT in kerosene or other solvent so as to leave a good residue.

Several species of the Calliphoridae live, during the larval stage, in the nests of birds and suck the blood of the nestlings. Here belong *Protocalliphora avium, P. hirudo,* and other species.

THE FAMILY MUSCIDAE

To this family belong many nonbloodsucking flies in which the arista is plumose to the tip (Fig. 171), the first posterior cell is narrowed or closed toward the margin of the wing (Fig. 172), and the hypopleural bristles are absent. The flies are nonmetallic in coloring, usually grayish or dark-colored. Comparatively few species of this group have been associated with myiasis.

Musca domestica Linn., the common housefly (see Chapter XVI for a full account), or rather its larva, has been reported many times as causing human intestinal myiasis. As the housefly normally breeds in a great variety of decaying vegetable matter, manure of nearly all kinds, etc., human infection must take place through drinking or eating contaminated liquids or foods or the flies actually oviposit on the soiled anus (as in the case of ill-kept infants). The eggs or young larvae are swallowed or pass into the rectum, and apparently development can continue in the human intestine. The actual disturbance caused by the presence of the larvae is probably not very great but we have no well-defined infection fully recorded. The great majority of cases have been reported from infants. Jones (1913) removed about thirty living larvae from the stomach of a patient suffering from a hepatic abscess. Recently Rennie (1927) has described a case of intestinal myiasis in a breast-fed baby in Scotland. Leon (1921) reports a peculiar case of urinary myiasis in a young man (22 years of age) in Romania. The patient, suffering from blennorrhagia, had evidently been infected by the housefly ovipositing in the discharge during his sleeping hours. In all, 17 larvae of *M. domestica* were passed in his urine. Mumford (1926) describes two cases of urinary myiasis in infants, one in a male and the other in a female. In the first case the infection was prolonged, the child suffered from convulsions and severe pain at micturition and, in all, passed several hundred larvae. Treatment with urotropine resulted in the passage of only dead larvae and the apparent recovery of the child. The second case is not so clear as the larvae and well-developed eggs were found on the diaper soiled with urine. No adult flies were reared and the sickly child died. At Ithaca about 100 living larvae of the housefly were removed at autopsy from the small intestine of a pig (August 1944).

Muscina stabulans (Fallen), the nonbiting stable fly (Fig. 192), is one of the common flies about barns and it also occurs in houses. The species is widely distributed throughout the world. It is slightly more robust than the housefly, dark gray in color, with two rather distinct medium dark lines and two lateral indistinct lines on the thorax (quite similar to the housefly); the abdomen is dark gray with lighter markings. The venation (Fig. 193) is quite distinct and will aid in its identification. This species breeds in decaying fruit and vegetables, manure, human excrement, raw and cooked meats, decaying carcasses, dead insects, and similar substances. The larva looks like a typical housefly maggot but can be distinguished by the posterior spiracles. Each spiracular plate (Fig. 194 *4*) is round, small, with a wide peritreme, and the three short slits are directed toward the median line. The larvae of this species are known to cause human intestinal myiasis. Portchinsky (1913) records severe abdominal pains, bloody stools, nausea, and vomiting associated with an invasion of this larva. The patient continued to suffer for about five months. After treatment 50 living larvae were expelled. The patient recovered but was later troubled with intestinal catarrh. Brand (1931) reports an interesting case in a child only 15 months old. When brought to the doctor for treatment the child was suffering from convulsions and general debility. After five weeks' treatment with ultraviolet irradiations and increased diet it was discovered that the child was passing "worms." The mother, during the sixth week, brought in a fresh stool and it was found alive with maggots and numerous pupal cases. The larvae proved to be *Musca domestica* but the pupal cases all gave forth *Muscina stabulans* (wrongly recorded in Brand's article as *Stomoxys stabulans*). No specific treatment seems to have been given. On October 12, about ten weeks after the first maggots were observed, the family moved into another home and the infection suddenly ceased. Three months later the child had apparently almost completely recovered. How the child became infected and continued to pass maggots for such a long time is not explained. The sudden spontaneous cure could be explained by the season of the year; these flies do not breed after the first of October in central New York. Franchini (1927) records a case in a man 25 years of age. At intervals during two years the patient suffered from pruritus ani and abdominal pains, and passed loose, mucoid, and at times bloodstained stools. Treatment with stovarsol resulted in the discharge of larvae of *Muscina stabulans* and the patient recovered.

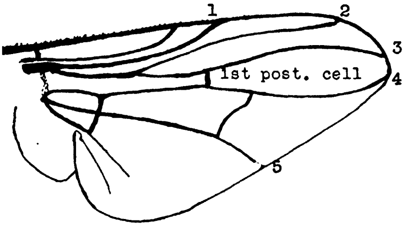


Fig. 193. Wing of *Muscina stabulans.*

THE FAMILY ANTHOMYIIDAE

The anthomyids are common and abundant flies. The larval habits are extremely varied, many developing in decaying vegetable matter, others in living plant tissues, and some in animal excrement; a few are parasitic. The larvae of certain species attack onions, radishes, and turnips or mine in the leaves of spinach, lettuce, swiss chard, and other greens, and these may be eaten. Several species are known to cause intestinal myiasis when taken into the alimentary tract with food or by accident.

Fannia canicularis (Linn.) is the so-called "lesser housefly" (Fig. 196) and may be seen commonly hovering in mid-air or flying hither and thither in our homes. It is a grayish fly, measuring from 5 to 6 mm. in length. It breeds in all kinds of decaying vegetable and animal matter and in the excrement of horses, cows, and man. It is frequently found in decaying grass piled up on lawns. The eggs hatch in about 25 hours, and the larvae complete their growth in about a week if food, moisture, and temperature are favorable.

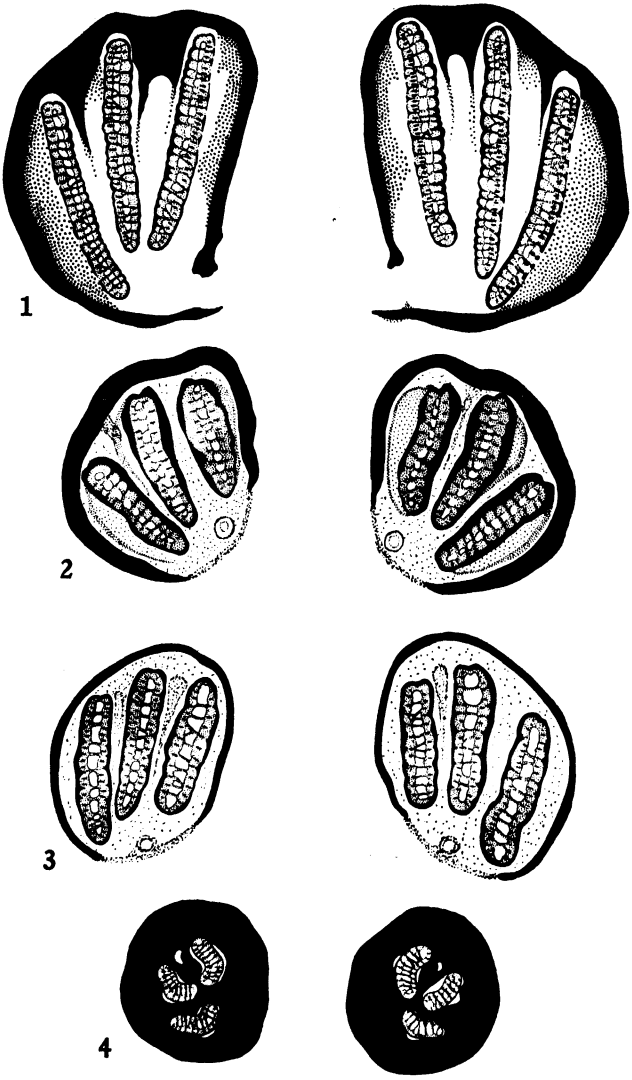


Fig. 194. Posterior spiracular plates of mature larvae. (*1*) *Sarcophaga bullata.* (*2*) *Callitroga macellaria.* (*3*) *Wohlfahrtia vigil.* (*4*) *Muscina stabulans.* (All drawn to the same scale showing the relative size and distance apart on the larvae.)

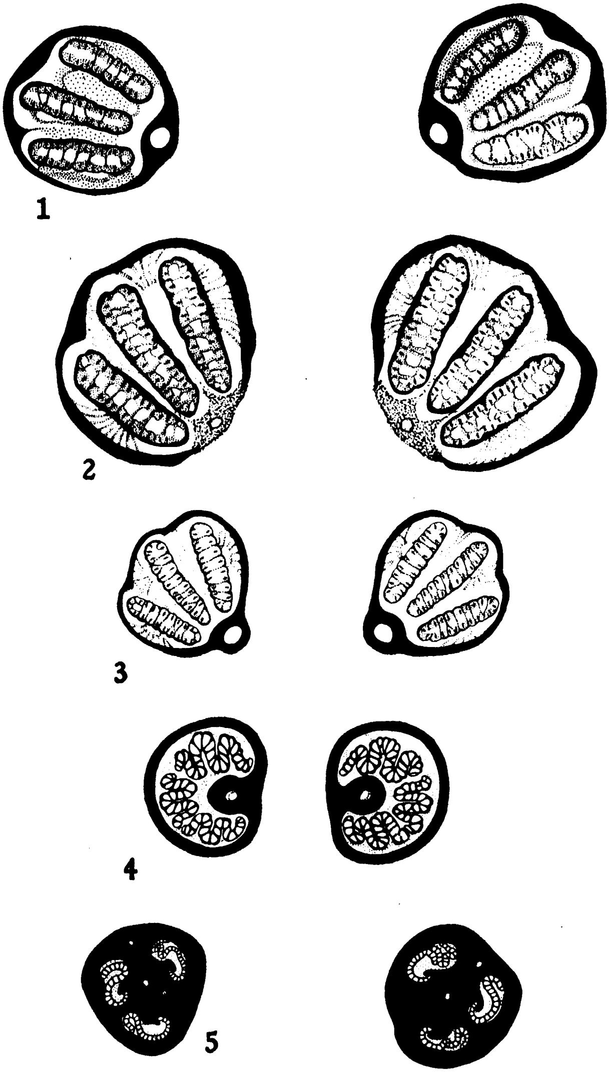
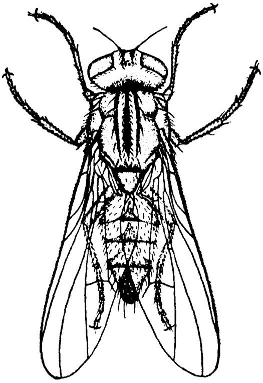
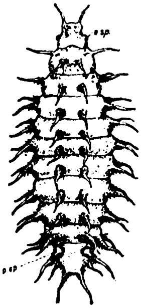


Fig. 195. Posterior spiracular plates of mature larvae. (*1*) *Calliphora vomitoria.* (*2*) *Phormia regina.* (*3*) *Lucilia sericata.* (*4*) *Musca domestica.* (*5*) *Stomoxys calcitrans.* (All drawn to the same scale showing the relative size and distance apart on the larvae.)

Otherwise the larval life may be prolonged to three or four weeks. The larva (Fig. 197) is very characteristic and may be recognized by its flattened appearance and spinelike appendages. It measures from 5 to 6 mm. in length. The pupal period occupies about a week. The species is widely distributed throughout the world.

Fannia scalaris Fabr. has been called the "latrine fly" on account of its most common breeding habitat. In appearance the adult is almost identical with that of the lesser housefly. It can be distinguished from it by the middle tibia, which possesses a distinct tubercle. The females select excrement of man and animals for the placement of their eggs. The eggs hatch in about 24 hours and the larval growth is completed in 6 to 12 days. The larva (Fig. 198) is very distinctive. It is flattened dorsoventrally and bears spiny processes that are somewhat feathered. Viewed from above the larva appears to be surrounded by a fringe of featherlike appendages. The pupal period occupies about nine days.





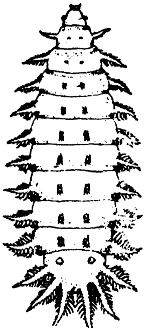


Fig. 196 (*left*). *Fannia canicularis* L., the lesser housefly. Female.

Fig. 197 (*center*). Larva of *Fannia canicularis.* (From Hewitt, *The Housefly,* by permission of the Cambridge University Press.)

Fig. 198 (*right*). Larva of *Fannia scalaris.* (From Hewitt, *The Housefly,* by permission of the Cambridge University Press.)

INTESTINAL AND GASTRIC MYIASIS: There are numerous records of the larvae of both these species causing gastric and intestinal myiasis of man. Hewitt (1912) gives a brief summary of the known cases. He states, "The presence of these larvae in the stomach is usually indicated by nausea, vertigo, and violent pains; the larvae in many cases are expelled by vomiting. If they occur in the intestine, they are expelled with the feces and their presence is signalised by diarrheal symptoms, abdominal pains, or hemorrhage caused by the traumatic lesions of the mucous membrane of the intestine which the larvae affect."

In addition to invading the intestines, the larvae of *F. canicularis* have been recorded from the urethra of both males and females. Chevril (1909) summarized all known cases (20) and concluded that six were genuine, ten were probable, and four doubtful. He also gave an additional case of a woman who suffered from albuminuria and urinated with difficulty. Later she discharged 30 to 40 larvae of *F. canicularis* in her urine and apparently recovered. King (1914) reports a case of urethral myiasis in a young man in Virginia due to the larvae of *F. scalaris*. Three larvae were passed at different times. Mumford 1926) gives an account of a severe case of urinary myiasis in a young male baby in England due to the larvae of *Fannia canicularis* and *Musca domestica*. The infection was prolonged and several hundred larvae were passed. Detwiler (1929) reports a case of urinary myiasis in western Ontario due to the larvae of *F. canicularis*.

MODE OF INFECTION: All the larvae of anthomyids so far reported as causing gastric, intestinal, and urogenital myiasis belong to the two species described above. These species normally breed in animal excrement and decaying vegetable and animal matter. Such larvae can apparently continue their growth in the alimentary canal of man. Man probably becomes infected from eating decaying fruit, food soiled with excrement, or other contaminated matter on which the eggs had been laid or in which very young larvae were present. Hewitt suggests that in open privies the flies are attracted to unclean persons and deposit their eggs about the anus or the external genital orifice (especially of females); the eggs hatch and the larvae migrate into the intestines or up the urethra. In young children infection may occur by direct oviposition about the anal opening, especially on those that are unclean and left exposed. In adults such infection may take place during sleep or a drunken stupor or while lying in the open uncovered and unclean. These are common flies in sleeping rooms during the warm season and direct infection can easily take place under certain conditions.

THE FAMILY OESTRIDAE

In recent years the family Oestridae has been restricted to a small group of flies, the larvae of which are parasitic in the nasal region and frontal or maxillary sinuses of sheep, goats, horses, antelopes, and other hoofed mammals. Rarely the first-stage larvae are reported from man, entering the eye, nose, or mouth. The groups separated from the original family include the Cuterebridae, warble-producing larvae in a variety of mammals as rabbits, rodents generally, domestic and wild mammals, and man and the Hypodermatidae, the well-known warble flies of domestic cattle and deer. The adults of these three families may be recognized by the following brief key:

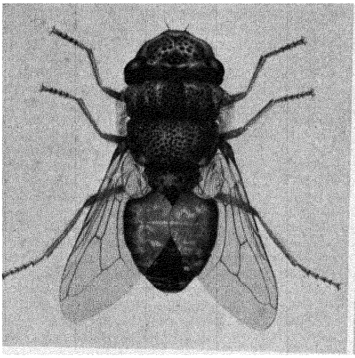
1. Postscutellum well developed; squamae large; apical cell greatly narrowed or closed at margin of wing 2
   Postscutellum not developed; squamae large and apical cell narrowed at margin .... *Cuterebridae*
2. Apical cell closed and petiolate (Fig. 199) .... *Oestridae*
   Apical cell open, though narrowed at the margin (Fig. 204) .... *Hypodermatidae*

The larvae of these three families are usually easily recognizable and the separating characters are given on pages 531–533.

The Oestridae possess two genera that are of some importance in medical entomology, *Oestrus* and *Rhinoestrus*. *Oestrus ovis* Linn. is the sheep nasal botfly. The adult (Fig. 199) measures from 10 to 12 mm. in length. The head is large, more or less yellowish; the thorax is dark with numerous deep, black pits and overlaid by a grayish bloom; the abdomen is almost black and the legs are yellow. The species is widespread through the world and is a serious pest in sheep-producing countries. The adults do not feed. The females in flight dash at their hosts (principally sheep and goats) and deposit living larvae in or near the nostrils. These pass up the nostrils and enter the sinuses. Here the larvae complete their development and when mature drop or are sneezed out. Entering the ground to pupate, the adults emerge in three or four weeks. The growth of the larvae in the sinuses may be very rapid, as short as 2½ months or less in warm climates or may be prolonged throughout the winter in colder climates. In Europe there is said to be but one annual generation, but in North America there are evidences of two annual generations.

Though primarily a pest of sheep and goats, these flies have caused many human infections, especially among sheep and goat herders about the Mediterranean Basin and parts of Russia. The fly discharges its living larvae into or near the eye. The maggots penetrate the conjunctiva and produce a painful conjunctivitis. As these larvae cannot develop in man beyond the first stage, the finding and removal of the maggots results in immediate cessation of pain and cure. The larvae have also been reported as causing myiasis of the nose and throat, the flies discharging their larvae into the nose or mouth. These infections are painful but as the larvae cannot complete their development the cause of trouble, often very severe, disappears in a week or two unless secondary infections develop. Dupuy d'Uby (1931) gives detailed accounts of case histories of man.

Rhinoestrus purpureus (Brauer) is normally a parasite of horses, mules, zebras, and other Equidae. It is widespread in Africa, southern Europe, the Near East, India, extensive areas in Russia, Mongolia, Manchuria, and parts of China. Human cases of eye infection have been reported by Portchinsky (1915).



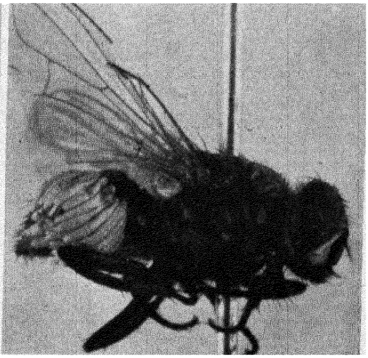


Fig. 199 (left). The sheep nose fly, *Oestrus ovis*. (Courtesy Department of Agriculture, Division of Entomology, Canada.)

Fig. 200 (right). An anthomyiid fly carrying a mass of eggs of *Dermatobia hominis*.

THE FAMILY CUTEREBRIDAE

The Cuterebridae (the warble flies of rodents, man, and deer) is a comparatively small family of very important flies. The adults (Fig. 201) are rather large and appear like bees, some like bumblebees. The mouth opening is small and the mouth parts are usually vestigial. The adults of many of the species are not commonly observed except by those who seek them. All the species are parasitic on mammals during their larval stage. Parasitism occurs in tumors or warbles under the skin (hence the name) or in the nasal and pharyngeal cavities.

Dermatobia hominis Linn., Jr. (*D. noxialis* Goudot, *D. cyaniventris* Macq.), the human warble fly (Fig. 201), is widely distributed and abundant in Central and South America and Mexico. The adult is 12 to 18 mm. in length; the head is mainly yellow, the thorax dark bluish gray, and the abdomen a brilliant dark blue. These flies are apparently rarely seen in nature. They occur most commonly in forested regions or along the margins of forests.

LIFE CYCLE: Sambon (1922) carefully describes the method of oviposition. The females select other species of arthropods, usually mosquitoes, various flies (Fig. 200), or even ticks as carriers of their eggs. They apparently seek out some shady, mosquito-ridden pool and await the emergence of the adult mosquitoes or capture a fly in the shade. When the mosquitoes fly away from their pupal cases, some of them are seized by the botflies. Each botfly quickly deposits 14 to 25 eggs and glues them to the abdomen of the mosquito or fly. (Fig. 200). The eggs are so placed that the ends through which the young maggots emerge are directed away from the mosquito host. Each egg contains a fully developed first-stage maggot ready for hatching. The mosquito most commonly used is *Psorophora* (*Janthinosoma*) *lutzii* Theo., a fierce, biting species and abundant in woodlands. *Psorophora posticata* Say is also said to be employed for oviposition purposes. Patton and Evans (1929) figure an anthomyid with a mass of *Dermatobia* eggs attached to her abdomen. Dunn (1918) records five separate infections of one individual with *D. hominis* through the probable agency of a tick (*?Amblyomma cajennense*). He also found the mature eggs on a species of *Limnophora* (Anthomyiidae) from which he infected himself. In addition to these, Neiva records *Musca domestica, Stomoxys calcitrans,* a tabanid, and sylvan muscids as carriers in Brazil.

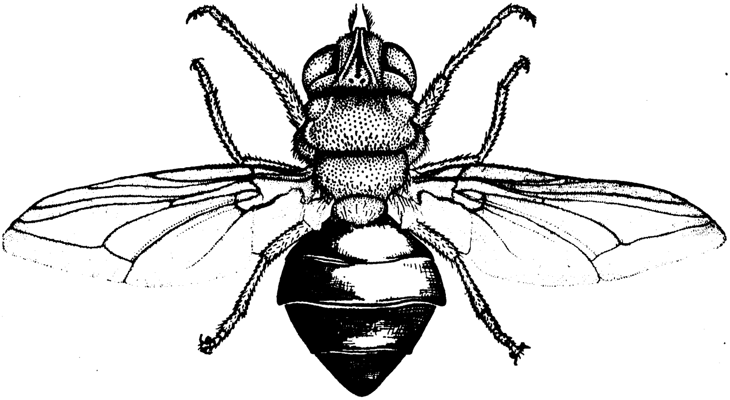


Fig. 201. The human botfly, *Dermatobia hominis.* Female.

When a mosquito or other insect bearing the eggs of *Dermatobia hominis* bites or visits man, the warmth evidently induces the maggots to burst open the eggshell. The young maggot bores directly into the skin, usually taking advantage of the puncture made by the mosquito or, as in the report of Dunn, the sites of tick bites. Busck (1913) reared the maggot on himself. He noted the infection on May 29 and on September 9, just 103 days later, the maggot left his arm fully grown. The maggot was placed in moist sand, pupation took place and the adult emerged on October 23. Busck states that the larva caused him little pain though the exuding wastes and serum were annoying and necessitated bandaging. At times the grub would rotate on its own axis and cause severe pain. During the infection Busck states that he required at least three to five hours more sleep each day; after the grub emerged his sleep requirements returned to normal. Dunn (1930) reports rearing six larvae on himself—two experimental infections on his left forearm (Fig. 203) and four natural infections at about the same time. All these infections were from eggs carried by an anthomyid fly, *Limnophora* species. Penetration of the unbroken skin took place in 42 minutes in one case and one hour and 35 minutes in the

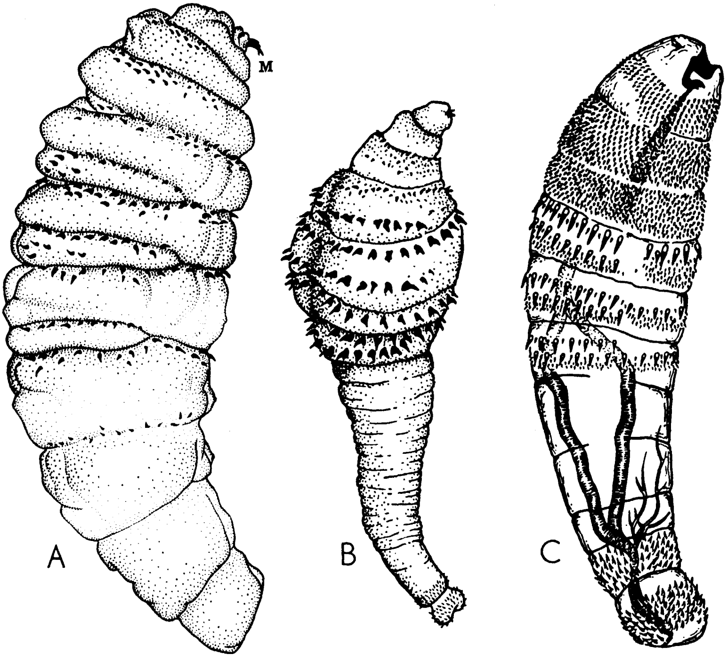
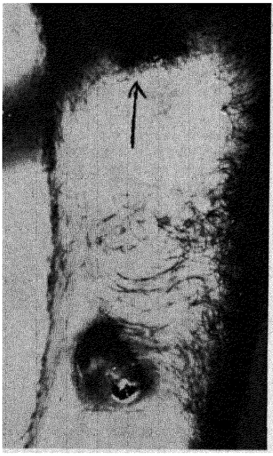


Fig. 202. Dermatobia hominis. (*A*) Full-grown larva after emergence. (*B*) Second-stage larva. (*C*) First-stage larva, greatly enlarged. M, mouth hooks. (*A* and *B* not to the same scale; *C* redrawn after Newstead and Potts.)

other. Dunn experienced considerable discomfort from occasional severe pains at the points of infection and muscular soreness and stiffness, while the exuding wastes required bandaging. The time required from the penetration of the skin till the emergence of the mature larva was 46 days and 15 hours in one case, 46 days and 21 hours in another, whereas two others required 50 days and 15 hours and 54 days and 18 hours respectively. After the larval emergence the lesions (Fig. 203) soon healed, leaving slight scars. The pupal period varied from 22 to 24 days.



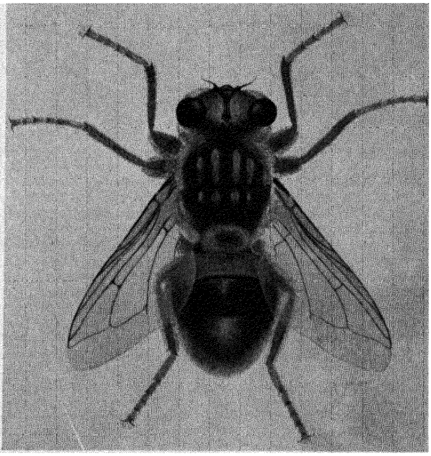


Fig. 203 (*left*). Lesions caused by the larvae of *Dermatobia hominis* reared on a man's arm. Upper lesion shown 8 hours after the larva had emerged, lower lesion 2 days before larva emerged. (Courtesy Mr. Dunn.)

Fig. 204 (*right*). The heel fly, *Hypoderma lineatum*. (Courtesy Department of Agriculture, Division of Entomology, Canada.)

The full-grown grub (Fig. 202 *A*) measures from 18 to over 24 mm. in length and is rather characteristically bottle-shaped—the narrow and tubular end (the neck of the bottle) constituting the posterior part; as the prepupal stage approaches, the maggot becomes more grublike (Fig. 202 *A*). The larval mouth hooks are very powerful and large. The body is well supplied with stout, short, backward-projecting hooks, very efficient for maintaining or shifting position in the flesh of the host. These hooks or spines are arranged as follows: on the segment back of the anterior spiracles there is a more or less double row of spines on the dorsum; the next segment bears a double row all around its anterior margin; the next (presumably the first abdominal segment) bears two belts of spines—a double row along the anterior margin and a dorsal row just back of the middle, which reaches the lateroventral angles; the next two segments are similarly armed; the next segment (4th abdominal) has an anterior row of small spines, double on the venter and several rows on the posterior margin on the dorsal side; the remaining segments are unarmed except the last two, which bear numerous small spines all over them. These small spines are directed backward and undoubtedly enable the larva to keep the skin of the host broken. The spiracles are located on rather weakly chitinized areas and each possesses three slits, directed ventrally and slightly toward the median line.

THE LESION: The lesion (Fig. 203) appears as a typical boil or warble. Within the boil the larva lives with the constricted end toward the surface—the spiracles being located on the tip. Usually a small scab forms over the apex of the boil but serum exudate and wastes are constantly discharged. The lesion is of long duration, from two to four months. If located near a joint or if it becomes secondarily infected, serious conditions may arise. The native treatment usually consists of opening the tip of the boil, applying tobacco juice, and then squeezing out the larva. Busck found that the larva could be removed easily by softening the boil, widening the aperture, and then carefully applying pressure well below the boil. In this way the larva can be forced out without the use of the surgeon's knife. It would seem that local freezing before squeezing out the grub would be the most effective treatment. After removal of the grub, the wound should be thoroughly washed and treated with antiseptics.

HOSTS: The principal hosts are domestic animals as cattle, dogs, cats, mules, pigs, donkeys, etc., and man.

PROPHYLAXIS: As this botfly attacks mammals primarily, efforts should be made to reduce their abundance in domestic animals. Navarro (1927) reports that in the eucalyptus forest regions near São Paulo, Brazil, the infestation is very severe. He gives the following infestation rates: man, 44 per cent (819 persons examined); cattle, 100 per cent; mules, 17 per cent; pigs, 12.3 per cent; horses, 9.3 per cent; and donkeys, 5 per cent. In parts of Mexico, Central America, and Panama severe infestation of cattle frequently occurs and human cases are not uncommon. In order to escape infection in regions where this fly is prevalent avoidance of mosquitoes, ticks, and bloodsucking and other flies is essential. Houses should be carefully screened and bed nets should be used. All small and persistent pimples should be carefully watched and treated.

THE GENUS *CUTEREBRA*

The adults look much like bumblebees. They are parasitic in their larval stages on rabbits and rodents (such as squirrels, chipmunks, field mice). The mature larvae are large, ovoid, and thickly set with spines or scales. They are known only from North America. Only two human cases of infection are apparently recorded. Beachley and Bishopp (1942) report a nasal infection in a woman in Virginia. A single first-stage larva of a *Cuterebra* species was squeezed out after causing severe pain. Bequaert (1945) describes an infestation of a man at Ware, Massachusetts. The maggot, 16 mm. in length, was removed alive from a boillike swelling below the right nipple. It proved to be *C. buccata* (F.), the rabbit warble (Fig. 213).

THE FAMILY HYPODERMATIDAE

Hypoderma bovis Linn. and *Hypoderma lineatum* (Villers) are the common ox warble flies of Europe, America, and other parts of the world. In northern climates the grubs may be found in swellings or warbles on the backs of cattle from early January to late April. When mature the grubs are very large and work themselves out of the swellings, dropping to the ground where they pupate. The adults (Fig. 204) are active during the summer months, depositing their large eggs on the hairs from the hocks to the knees and along the sides of the belly. The maggots enter the skin, where they hatch and proceed to migrate through various parts of the body and usually reach the wall of the esophagus during September, October, and November. From here they migrate through the connective tissue by various routes and eventually appear on the backs of the cattle in early January or later. Though these maggots are primarily parasites of cattle, there are numerous records of human infection both in Europe and America. Miller (1910) reported an interesting case in an eleven-year-old boy from Roanoke, Virginia. The boy was admitted to the Johns Hopkins Hospital on March 13, 1908, with a swelling under the chin. The excision of the swelling uncovered a second-stage larva of *Hypoderma lineatum*. The boy had noticed a lump below his left knee in December. This "lump" had migrated up his leg and abdomen, under the axilla, up the right side of the neck, and irregularly about the scalp, passing back of the ear to the submental region, which it reached in about two months. Here it remained stationary till excised. A second lump appeared on his groin in January, and this migrated upward till it reached the occipital region where it came to a head. The boy broke the scab and pulled out an active grub about one inch long. Style (1924) records a similar migrating infection in a four-year-old boy in England. In all he removed three grubs from swellings on various parts of the scalp. One of the grubs was definitely identified as the penultimate stage of *H. lineatum*. Of interest here is that the boy suffered severe pain as the swellings appeared and disappeared about the head. Lanford and Warner (1925) describe an infection of the testicle of a 22-month-old child. They removed three larvae from the tunica vaginalis. There is apparently no record of migration in this case. Herms (1925) reports infection due to *H. bovis* in a cowboy. The grub migrated from the groin over the body and became localized on the shoulder, where the grub was squeezed out. Six months later a second grub emerged from a swelling on the thigh. Another case of infection is reported by André (1925) in a young child in Upper Savoy. The grub was removed from a swelling behind the ear. Toomey, Topsent, Wegelin, and Condorelli report other cases from Europe. These grubs can only be identified by a close study of the posterior spiracles (Fig. 205).

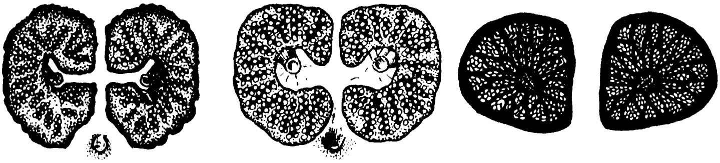
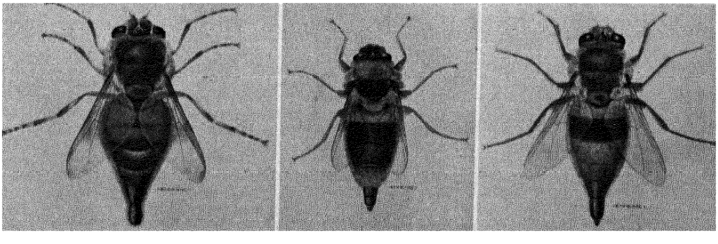


Fig. 205. Posterior spiracles of larvae. *Left: Hypoderma bovis. Center: Hypoderma lineatum. Right: Oestrus ovis.*

THE FAMILY GASTEROPHILIDAE

The adults of the botflies of horses (Figs. 206–208) can be easily recognized by their general likeness to honeybees and their persistent flight about horses during the summer months. The larvae of at least three species of world-wide



Figs. 206, 207, 208. Adults of *Gasterophilus* species. *Left to right: G. intestinalis, G. haemorrhoidalis, G. nasalis.* (Courtesy Department of Agriculture, Division of Entomology, Canada.

distribution have been reported as causing myiasis in man under such terms as "creeping eruption," "larva migrans," subcutaneous myiasis, or other terms. In all known cases the infection was due to invasion by the first-stage larvae. The three species involved are *Gasterophilus intestinalis* (de Geer), *G. nasalis* (Linn.), and *G. haemorrhoidalis* (Linn.).

The botflies lay their eggs on the hairs (Fig. 209); *G. intestinalis* on various parts of the body, usually inside the knees; *G. haemorrhoidalis* about the lips and mouth; and *G. nasalis* under the jaw. By accident they may be deposited on the hairs of man. Tamura (1921) summarizes 43 reports from literature and of these the causative agent was determined in only six cases. Four cases of "creeping eruption" due to the larvae of *G. intestinalis* and one caused by the larva of *G. haemorrhoidalis* have been reported from America. Of these, four were from Manitoba and Saskatchewan and one from Nebraska. Austmann (1926) gives an interesting account of his case. The larva was located in the forearm and the physician saw the case about four weeks after the beginning of the infection. The larva migrated at about the rate of 1.5 cm. per day. Iodine treatment for two weeks failed. Then the physician cleared the skin with light machine oil, observed the active larva in the skin, and removed it with a needle. The larva proved to be the first instar of *G. intestinalis*. Montgomery (1930) describes a *Gasterophilus* infection in an elderly farmer in Minnesota and gives an extended account of the lesion and the pathology of the infection. Several cases of "creeping eruption" due to *Gasterophilus* larvae have also been reported from Russia. In order that physicians may recognize these larvae, illustrations of the three common species are given (Fig. 210) and the typical posterior spiracles (Fig. 212).

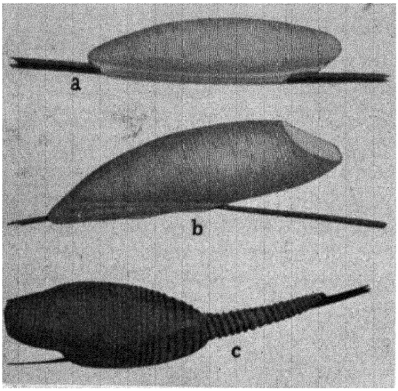


Fig. 209. Eggs of botflies as laid on hairs. (*a*) *Gasterophilus nasalis.* (*b*) *G. intestinalis.* (*c*) *G. haemorrhoidalis.* (After Hadwen and Cameron.)

THE FAMILY SYRPHIDAE

The Syrphidae constitute one of the largest families of flies. The great majority are brightly colored flies and love the sunshine. On account of their flight habit—remaining continuously on the wing and hovering near the same spot—they have been called "hover flies." Some species closely resemble bees, especially the drone bees, wasps, or hornets. The most distinguishing character of the adults is the presence of the spurious vein (Fig. 211, Sp.) in the wing. In this family practically only two genera, *Tubifera* (*Eristalis*) and *Syrphus,* need be considered.

Tubifera (*Eristalis*) *tenax* (Linn.), the drone fly, is a rather large fly (Fig. 211) resembling the drone bee. The adults may be seen flying over open cesspools, water heavily charged with rotting animal matter, and liquid manure and about open privies, the effluent from septic tanks, etc., near or on which they deposit their eggs. The larvae are very distinctive (Fig. 211) and are known as "rat-tailed maggots." Though their larval habitat should mitigate against human infection, a rather large number of cases of intestinal myiasis of man caused by the larvae of this or related species is on record. Hall and Muir (1913) carefully investigated all known cases and listed 13, 12 intestinal and 1 nasal. In 1918 Hall recorded another case in a boy 18 years of age. This patient passed a rat-tailed maggot in his stool. The symptoms were intense irritation of the rectum. At this time a total of 20 cases were listed—18 in man

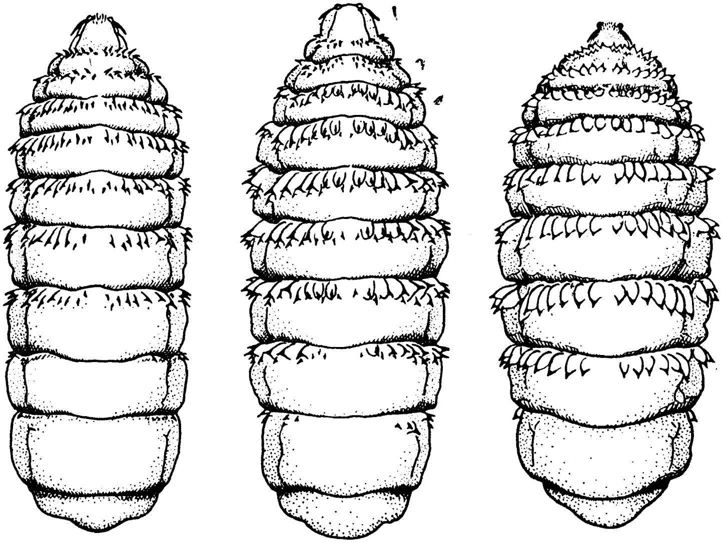


Fig. 210. Larvae of *Gasterophilus* species. *Left: G. haemorrhoidalis. Center: G. intestinalis. Right: G. nasalis.*

(16 intestinal, 1 nasal) and 2 (vaginal) in cows. Since then Pumpelly has reported a case in a man 30 years of age, residing in Virginia. The patient, suffering from constipation, had passed worms in his stools. Treatment with carbon tetrachloride resulted in the evacuation of six larvae, all *Tubifera tenax* (?). Another case has been reported from Argentina, a 15-month-old child evacuating larvae after treatment, and one from the Federated Malay States. Bruce has also reported a case of vaginal myiasis in a cow in British Columbia. The vagina was diseased and the author thinks the fly deposited her eggs directly on the exudate. In all, 12 maggots were recovered. Swartzwelder (1942) reports removing 7 maggots after treatment of a six-year-old child in Louisiana.

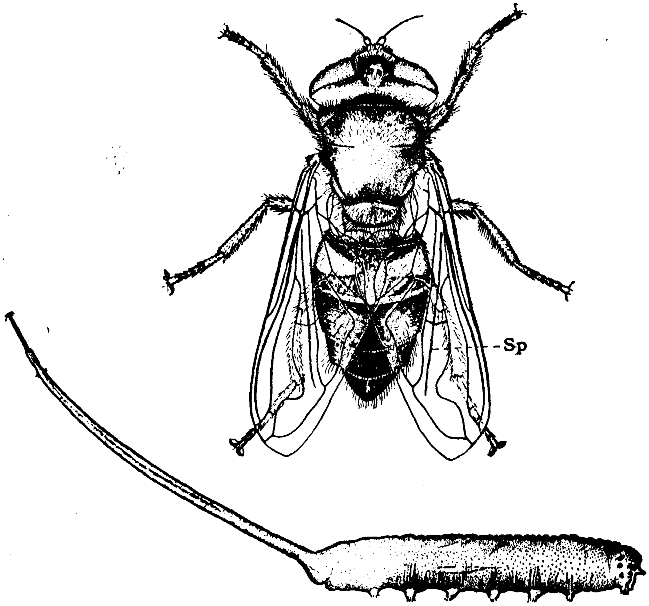


Fig. 211. The rat-tailed maggot, *Tubifer tenax*. *Upper:* The adult. *Lower:* The larva. Note the long telescoped breathing tube. Sp, spurious vein.

Infection with *Tubifera* larvae would seem only possible from drinking fouled water containing young larvae or eggs, from soiling the hands with wastes on which young larvae or eggs were present, from eating unwashed water cress obtained from filthy water, or in some cases from eating rotting fruit. Though *T. tenax* is the most commonly reported species whose larva causes myiasis, other species, *T. arbustorum* and *T. dimidiatus,* have also been incriminated. It may be pointed out here that species identification of *Tubifera* larvae is probably impossible at present. All specific references, except where the adult has been reared, should be regarded as doubtful. *T. tenax* is, however, our most common species, world-wide in distribution, and numerous cases of infestation have been reported.

Syrphus larvae have also been reported as causing intestinal myiasis by Austen, Patton, and Mumford. As the larvae of *Syrphus* are practically all predacious, feeding largely on plant lice, infection must have taken place from eating unwashed greens or vegetables as lettuce, spinach, celery, cabbage, etc., the larvae being swallowed along with the lice. In all human infections so far reported the *Syrphus* larvae were dead when evacuated.

OTHER CASES OF MYIASIS

Patton and Evans (1929) describe a urinary myiasis due to the larvae of *Psychoda albipennis* (family Psychodidae) in a young boy. One of the larvae was obtained directly from the bladder with the aid of the cystoscope. How infection took place is not clear, the authors conjecturing invasion through eating of infested soil and the passage of the larvae from the rectum to the bladder. Okada (1927) reports a gastric myiasis caused by the larvae of *Psychoda b. punctata* Curt. The patient, a girl of seventeen, vomited living larvae. Austen (1912) records an intestinal infection by the larvae of *Megaselia* (*Apiochaeta*) *scalaris*[3] (Phoridae). A European, resident in Burma, passed the larvae in his stools for about a year. The infection was supposed to have originated from infested candied bael fruit that he had eaten. Despite all precautions the patent continued to pass not only larvae every few months but puparia and, on one occasion, 8 to 12 flies. It is believed that the fly bred continuously in the intestine—the adults mating, eggs being deposited, and the cycle continuing. The fly is widespread in its distribution, breeds readily in decaying meat, animal matter of all kinds, various foodstuffs, dead insects, and similar substances. Patton records breeding generation after generation of the fly in small, corked glass tubes. He believes that this fly commonly causes intestinal myiasis but is overlooked because of its small size. Wright (1927) reports an interesting case of ophthalmomyiasis due to this fly in a patient in a hospital at Madras. The crusted keratitis of the cornea was thoroughly washed with sterilized saline solution and the crust then removed. It was broken up, cultures made on blood-smeared agar, and later subcultured.

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[3] Also called *repicta, xanthina, ferruginea, circumsetosa.*

In a week Wright found all his cultures infested with maggots. These were reared and the adults proved to be *Megaselia* (*Apiochaeta*) *scalaris.* Van Slyke (1932) found live eggs in stools of natives of the Belgian Congo and reared adults.

The larvae of the cheese skipper (*Piophila casei,* family Piophilidae) have been reported many times as causing a mild intestinal myiasis. The larvae normally live in cheese, hams, bacon, beef, smoked fish, and similar foods. The larva has the marked ability of coiling on itself, placing its mouth parts in the hollow just behind the posterior spiracles and then, by a sudden release, to jump considerable distances (6 inches vertically or 10 inches horizontally), hence the name "cheese skipper." As cheese is one of its favorite breeding grounds, man becomes infected by eating "maggoty" cheese, a dish considered a delicacy by some people. It also may be ingested from infected meat of all kinds. The larva is muscoid in shape, 6 to 8 mm. in length when mature, with a rather powerful, cephalopharyngeal skeleton. The posterior spiracles are situated at the ends of two processes on the dorsal surface of the eighth segment and appear as two separate brownish structures. Each spiracle is rounded with three straight slits that are directed inwards and backwards. Though this larva rarely causes much disturbance in the human intestinal tract, Alessandrini reports that it is very resistant to drugs and chemicals, that in many cases lesions and slight hemorrhages may occur owing to the abrasive action of the mouth hooks, and patients may suffer from colicky pains and headaches. Simmons (1927) states the larvae pass through the intestines of dogs alive and cause lesions. It is said to be common among soldiers in military camps.

Recently Shrewsbury (1930) reports a case of intestinal myiasis in a child due to the larvae of *Rhyphus fenestralis* Scop. The enteritis cleared up after the child passed some four larvae during a period of three weeks. Meleney and Harwood (1935) investigated a case of intestinal myiasis caused by *Hermetia illucens* Linn. (family Stratiomyidae) in a ten-year-old boy at Nashville, Tennessee. They reared the maggots that had caused irritation in stomach and intestine with fainting spells. Infestation probably came from eating raw fruit or vegetables. Canavan (1936) reports a similar case by this fly in a six-year-old boy. Irritation was severe with fever of 104° F., vomiting, diarrhea, and pains. With discharge of maggots the child recovered.

SCOLECIASIS

Infection by lepidopterous larvae is rather rare and the reported human cases are of doubtful validity. Hope (1840) designated this type of parasitism as scoleciasis and records some seven cases. The only seemingly reliable case is that of a boy who repeatedly ate raw cabbage and later vomited larvae of the cabbage butterfly, *Pieris brassicae.* As far as the writer is aware, no authentic cases are reported in recent literature.

CANTHARIASIS

Accidental myiasis by Coleoptera (beetles) has been designated canthariasis by Hope. He tabulated all known cases at that time. Instances of such invasions are not rare but most of them are of doubtful validity. Reported cases relate to the larvae of the Dermestidae (the larder beetles) or the Tenebrionidae (the food-infesting species). Infection probably occurs through the eating of cereals, breakfast foods, and so forth containing the eggs or very young larvae. Most of the cases refer to *Tenebrio molitor,* the common meal worm. This worm is one of the important hosts of the cysticercoid of the tapeworm, *Hymenolepis diminuta,* a parasite of rats, mice, and occasionally man. Hinman and Faust (1932) summarize the known cases in America—in all, 44 infections of this tapeworm in man. They also list the recorded cases of this meal worm from humans, some 18 cases, and report two new cases; one a woman who vomited a mature larva and the second a patient undergoing a tonsilectomy in whose tonsil a larvae was found. Palmer (1946) reports an infection in a four-month-old baby, never breast-fed. The infection lasted for over four months, the baby passing living larvae of this beetle at intervals. Infection is assumed from the feeding of infested precooked cereals. Liggett (1931) reports a peculiar rhinal myiasis in a young girl due to the invasion of larvae of *Attagenus piceus* Oliv. (the black carpet beetle). Several workers in India, South Africa, and Ceylon have reported a peculiar type of intestinal myiasis caused by the presence of scarabaeid beetles. The beetles (*Onthophagus bifasciatus, O unifasciatus,* and *Caccobius mutans*) were passed alive in the stools. The infections occurred only in young (three- to eight-year-old) children and the method of invasion may be surmised. Sharpe (1947) lists an unusual intestinal myiasis by *Ptinus tectus* (Ptinidae).

GROUPING OF MYIASIS-PRODUCING FLIES [4]

The following outline according to Patton (1921) presents more accurately our present knowledge of myiasis-producing flies. Such flies may be placed in three groups: (1) specific myiasis-producing flies, (2) semispecific myiasis-producing flies, and (3) accidental myiasis-producing flies.

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[4] For a complete list consult James (1947).

SPECIFIC MYIASIS-PRODUCING FLIES: In this group belong those flies that are obligatory parasites. They may cause various types of myiasis such as cutaneous, aural, nasal, and intestinal. The following list includes practically all the known flies that are obligatory parasites causing myiasis.

Cordylobia anthropophaga (Africa), *Chrysomya bezziana* (Africa, India, the Philippine Islands), *Wohlfahrtia magnifica* (Europe, Asia, Africa), *Wohlfahrtia vigil, Callitroga americana* (North America), and all species of the family Oestridae (including also the recently separated familes Gasterophilidae, Cuterebridae, and Hypodermatidae).

SEMISPECIFIC MYIASIS-PRODUCING FLIES: This group includes those flies, the females of which normally oviposit or larviposit on fresh or decaying animal or vegetable matter but may lay their eggs or larvae in sores, wounds, skin abrasions, diseased organs emitting foul discharges (as the nose, ears, genital, or other organs), etc. The females of such flies are apparently attracted by foul odors to their places of oviposition and hence any suppurating wound or foul discharge on a living animal may serve as the attractant. The following list includes the more important species of flies that have been found invading human tissues:

CALLIPHORIDAE—*Callitroga* (*Chrysomya*) *macellaria, Chrysomya bezziana, Calliphora vomitoria, Calliphora vicina* (*erythrocephala*), *Lucilia sericata, Lucilia caesar* (?), *L. illustris, Phormia regina;* MUSCIDAE—*Musca domestica, Muscina stabulans.* SARCOPHAGIDAE—*Sarcophaga haemorrhoidalis, Sarcophaga fuscicauda, Sarcophaga chrysostoma, Sarcophaga* spp. ANTHOMYIIDAE—*Fannia canicularis, Fannia scalaris.* PHORIDAE—*Megaselia* (*Apiochaeta*) *scalaris.*

ACCIDENTAL MYIASIS-PRODUCING FLIES: In this group belong those flies whose eggs or larvae are, in some way, taken accidentally into the alimentary tract of man; or, in some cases, the flies may oviposit on the fouled anal region or urinary organs and the larvae thus gain entrance. The following list gives the more important species of flies reported from the alimentary tract or urinary organs:

MUSCIDAE—*Musca domestica* (intestinal and urinary myiasis), *Muscina stabulans, Stomoxys calcitrans* (intestinal myiasis). ANTHOMYIIDAE—*Fannia canicularis* and *Fannia scalaris* (intestinal and urinary myiasis). SARCOPHAGIDAE—*Sarcophaga haemorrhoidalis, S. fuscicauda, Sarcophaga* spp. (all intestinal myiasis). SYRPHIDAE—*Tubifera tenax, T. dimidiatus, T. arbustorum, Syrphus* spp. (all intestinal myiasis). PHORIDAE—*Megaselia* (*Apiochaeta*) *scalaris* (intestinal myiasis). PIOPHILIDAE—*Piophila casei* (intestinal myiasis). RHYPHIDAE—Rhyphus fenestralis (intestinal).

In conclusion it should be pointed out that many records of gastro-intestinal infections by fly larvae are certainly doubtful. Causey (1938) fed larvae of six different species of flies to dogs and in all cases the larvae were found either dead or partially digested in the stomach and intestines. None passed through the fecal wastes alive.

FLY (BLOWFLY) LARVAE AS SURGICAL AIDS

Recently, in fact since World War I, the late Dr. William S. Baer of Baltimore has employed maggots (blowfly larvae) for the treatment of chronic osteomyelitis. This treatment was the result of observations made during the war. He noted that deep wounds, caused by various missiles, yielded more readily to treatment when infected with maggots. The maggots devoured the dead and dying tissues and, probably at the same time, destroyed the invading bacteria. Thus the wounds became rather thoroughly cleansed and healing took place. The work with fly maggots for deep-seated wounds was developed and proved highly successful. More recently, other and equally effective methods have been devised and maggot treatment is, apparently, not practiced.

KEY TO THE THIRD-STAGE LARVAE OF THE MORE COMMON FLIES THAT CAUSE MYIASIS[5]

1. Larva typically resembling that of the housefly (Fig. 173); the body slender, cylindrical, tapering anteriorly and more or less truncate posteriorly 2

   Larva large, stout, resembling that of the cattle warble, *Hypoderma* spp.; cylindrical or more or less flattened, depressed or pear-shaped (Fig. 202 9

   Larva with spiny or fleshy lateral, dorsal or terminal processes (Figs. 197,198) 16

2. Last apparent segment (anal) with a deep concavity in which are located the spiracles (Fig. 182); each dorsal cornua of pharyngeal sclerite with a deep, posterior incision (Fig. 184) . . . . *Sarcophagidae* (*Wohlfahrtia* spp., *Sarcophaga* spp.)

   Last apparent segment (anal) without such a deep concavity; spiracles more or less flush with the posterior face of the anal segment; dorsal cornua of pharyngeal sclerite without an incision 3

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[5] Keys to the first- and second-stage larvae are omitted because they are not of sufficient accuracy to warrant their use. Such larvae should be submitted to specialists. For more detailed keys to species consult James (1947).

3. Slits of posterior spiracles sinuous, short or rather long, with the button area usually deep in the peritreme (Fig. 195, *4, 5*) .. *Muscidae* (in part) 4

Slits of posterior spiracles long, slender, and nearly parallel to each other (Figs. 194,195) and directed to button area .... *Calliphoridae* (in part) 6

4. Posterior spiracles D-shaped; three sinuous slits in each spiracle plate (Fig. 195, *4*) .... *Musca domestica*

Posterior spiracles not D-shaped; rounded or somewhat irregular 5

5. Spiracular slits slightly curved and surrounded by a large, dense peritreme (Fig. 194, *4*) .... *Muscina stabulans; M.* spp.

Spiracular slits S-shaped with a dense peritreme; button in the center (Fig. 195, *5*) .... *Stomoxys calcitrans*

6. Peritreme of posterior spiracles complete and with a distinct button (Fig. 195, *1, 3*) .... *Calliphora, Lucilia, Cynomyopsis,* spp.

Peritreme not complete and button weak, scarcely discernible or in a thinner area of peritreme 7

7. Posterior spiracles with button located in a thinner area of the peritreme (Fig. 195, 2) .... *Phormia regina*

Posterior spiracles lacking a button, not indicated 8

8. Tracheal trunks extending from posterior spiracles not pigmented (Fig. 187) .... *Callitroga macellaria*

Tracheal trunks extending from posterior spiracles deeply pigmented for some distance (Fig. 187). The true screwworm of America .... *Callitroga americana*

9. Each posterior spiracle with three distinct slits (Fig. 194 *1, 2, 3*) 10

Each posterior spiracle with numerous small openings but without well-defined slits (Fig. 205) 13

10. Larva pear-shaped (Fig. 202) and heavily spined; spiracular slits straight and sunk in a deep cavity .... *Dermatobia hominis*

Larva ovate; spiracular slits bent at the middle and at most in a shallow cavity (Fig. 212) .... *Gasterophilidae* 11

11. Spines on the anterior margins of the segments stout and in a single row (Fig. 210) .... *G. nasalis*

Spines on the anterior margins of the segments arranged in a double row 12

12. Spines small, tapering to a fine point; spines absent on dorsum of segment 11 and middle portion of segment 10 (Fig. 210) .... *G. haemorrhoidalis*

Anterior row of spines stout, blunter, larger; spines present on dorsum of segment 10 and a few each side of dorsum of segment 11 (Fig. 210) .... *G. intestinalis*

13. Mouth hooks poorly developed .... *Hypodermatidae* 14
    Mouth hooks well developed 15
14. Posterior spiracles with the stigmatal plate deeply cleft, funnellike toward the button (Fig. 205) .... *Hypoderma bovis*
    Posterior spiracle with the stigmatal plate more shallowly cleft toward the button (Fig. 205) .... *Hypoderma lineatum*
15. Mouth hooks hornlike; body with weak spines; posterior spiracles heavily sclerotized with button in the center and part of the plate (Fig. 205) .... *Oestrus ovis*
    Mouth hooks not so stout; body thickly set with spines or stout scales (Fig. 213); posterior spiracles divided into plates ...... *Cuterebra* spp.

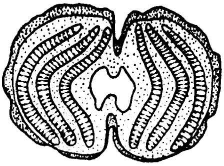

Fig. 212 (left). The posterior spiracles of a larva of *Gasterophilus intestinalis.*

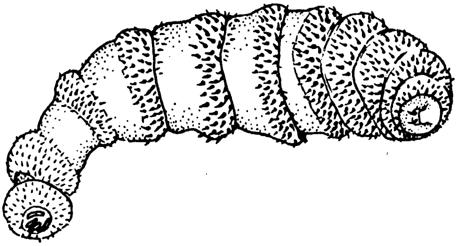

Fig. 213 (right). Second-stage larva of *Cuterebra buccata.*

16. Larva cylindrical, stout, with a long, posterior tubular extensible process. (Fig. 211) .... *Tubifera* spp.
    Larva not cylindrical; posterior extensible process lacking; with lateral and dorsal fleshy processes or spines 17
17. The fleshy processes more or less feathered (Fig. 198) .... *Fannia scalaris*
    The fleshy processes simple, more spinelike (Fig. 197) .... *Fannia canicularis*

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CHAPTER XVIII

The Siphonaptera: Fleas

FLEAS are small wingless insects (Figs. 217,221) in which the body is strongly compressed so that the vertical diameter is great, the transverse small. The mouth parts are formed for piercing and sucking; the metamorphosis is complete.

Fleas are all, in the adult stage, ectoparasites of warm-blooded animals—mammals and birds (one species has been recorded from a snake). They live among the hairs and feathers and in the nests of their hosts. Their compressed bodies, their long legs, and their hard, smooth exoskeleton give them unique advantages for life as external parasites. Fleas visit their hosts primarily for food, both males and females being bloodsuckers. The larval life is spent in the nests, burrows, or other habitats of their hosts. Usually each animal species or group of related species has its own particular fleas; though fleas, unlike many parasites, may pass from host to host with considerable indifference—as, for example, cat and dog fleas readily attack man; rat fleas will readily pass to other animals and to man in the absence of their own hosts.

EXTERNAL ANATOMY

The body of a flea is composed of the usual insect parts—a head, a thorax of three segments, and a ten-segmented abdomen. The last three segments of the abdomen are modified for sexual purposes. Fig. 214 outlines, somewhat diagrammatically, the main features of the external structures of a flea.

The head in most species is roughly triangular in lateral outline (Fig. 214). The posterior border articulates with the thorax. The ventral border (*Ctenocephalides canis*) is armed with stout, backward-projecting spines, the ctenidium or genal comb (Fig. 222 *b*). The antennal groove, situated just behind the eye, divides the head into two regions—the anterior called the frons, the posterior the occiput. The antennal grooves, in this species, do not unite on the middorsal line. Within the groove lies the antenna (Fig. 214 Ant). The antenna is composed of three segments, the last one of which is larger and

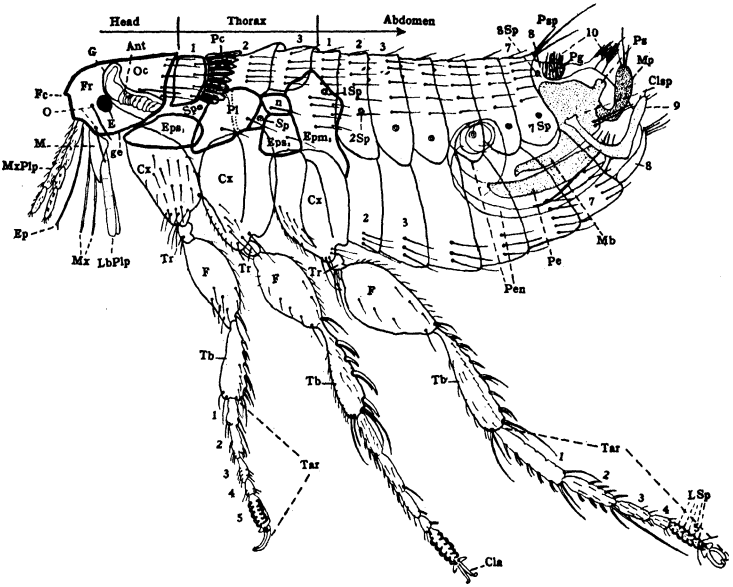


Fig. 214. A somewhat diagrammatic lateral view of a male flea showing the main structures used in identification. Ant, antenna in antennal groove (G); Cla, claw; Clsp, clasper with its movable finger (Mp) and the immovable process (Ps); Cx, the coxae; E, eye; Ep, epipharynx; Epm$_3$, epimeron of the third thoracic segment; Eps$_1$ and Eps$_3$, episterna of the first and third thoracic segments; F, the femur; Fc, frontal notch; Fr, the frons; G, groove for the antenna; ge, gena on which the genal comb is located when present; LbPlp, labial palpi; LSp, lateral spines on the last tarsal joint (also called plantar spines); M, maxillary plate; Mb, manubrium of the clasper; Mp, movable process of the clasper; Mx, maxillae (lacinia of the maxillae); MxPlp, maxillary palpi; n, a portion of the tergum of the third thoracic segment; O, upper bristle is the occular, lower the oral; Oc, occiput; Pc, prothoracic comb or ctenidium; Pe, penis plate; Pen, penis with the coil of springs; Pg, pygidium; Pl, pleuron of the second thoracic segment; Ps, immovable process of the clasper; Psp, antepygidial bristles or spines; Sp, spiracles of the meso- and metathoracic segments; 2Sp–8Sp, spiracles of the abdomen; Tar, tarsus, each with five segments (1–5); Tb, tibia; Tr, trochanter. (The numerals indicate the terga, 1–3, 1–10, and the sterna, 2–9, of the thorax and abdomen.)

longer than the others and is called the club (Fig. 51). The club is divided into a number of pseudo-joints by posterior indentations. In some species the club is divided into distinct subsegments. In front of the antenna is the eye, a dark, pigmented spot. In fleas there are no compound eyes and frequently eyes are entirely lacking. In some fleas the antennal grooves are connected by a deep constriction that renders the frons capable of independent movement—

such fleas are known as the broken-headed fleas; the great majority of fleas do not possess this constriction and the frons is not capable of independent movement. Frequently the constriction is represented by a thickening of the integument, the falx, but in many even this is absent.

The mouth parts (Fig. 215) are formed for piercing and are located at the anterior ventral margin of the head. These consist of: (1) the epipharynx (EP), a long, slender stylet, deeply concave on its posterior surface and lying in close approximation to the lacinia of the maxillae (the labrum is represented by a minute structure at the base of the epipharynx). (The mandibles are lacking.) (2) The maxillae, prominent structures consisting of a pair of palpi (MxPlp), a triangular plate (the maxillary plate, M), and a pair of elongated stylets (formerly called the mandibles) now known to be the laciniae of the maxillae (Mx). Each lacinia is a long, broad blade, convex on its outer surface, concave on the inner, and traversed by a strong midrib. The distal two-thirds of the outer wall is armed with rows of denticles directed toward its base. The

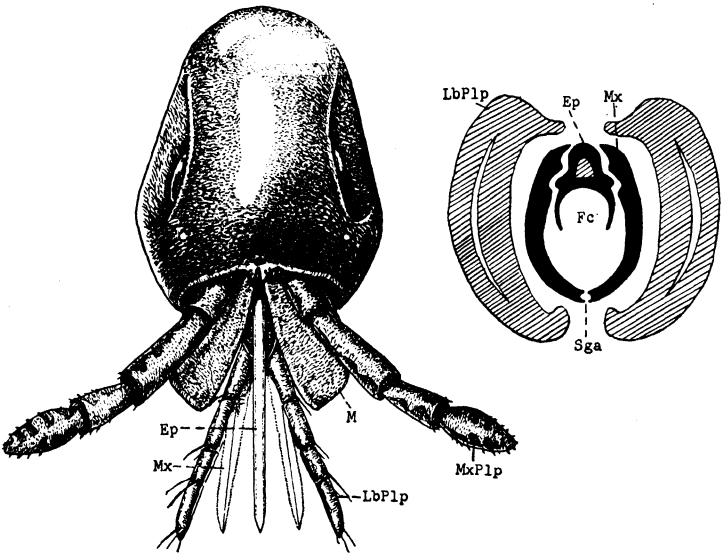


Fig. 215. Mouth parts of the flea. *Left:* Frontal view of head of flea with the mouth parts drawn out. *Right:* Cross section of the mouth parts. Ep, epipharynx; Fc, food channel; LbPlp, labial palpi; M, maxillary plate; Mx, lacinia of the maxilla; MxPlp, maxillary palpi; Sga, salivary duct.

margins of the laciniae are thin and fit closely together and to the epipharynx, forming the food channel up which the blood is pumped. (3) The labium consists of two lateral portions, the labial palpi (LbPlp), united at their bases forming the rostrum or proboscis. Each palpus is divided into segments, strongly concave internally, and so placed that the two palpi form a sheath or tube within which the epipharynx and the laciniae of the maxillae lie (Fig. 215). (4) Salivary glands are present with a distinct salivary pump. The secretion from the glands is injected into the wound down a canal formed between the laciniae (Fig. 215 Sga).

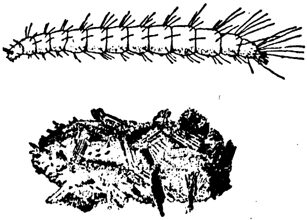
The action of the mouth parts has been differently interpreted by different workers. According to Patton and Cragg, the wound is made by the protraction and retraction of the bladelike laciniae. The maxillae (laciniae) and epipharynx are then driven into the wound thus made. The saliva is forced down the maxillary channel and the blood is pumped by the pharynx through the tube made by the laciniae and epipharynx, which are in close apposition.

The thorax consists of three well-defined segments, each segment bearing a pair of legs. A pair of spiracles is located just behind the pronotum and another pair between the meso- and meta-thorax. In the dog flea the posterior margin of the pronotum bears a row of large, black spines, the pronotal comb or pronotal ctenidium. The legs are well developed and adapted for leaping and rapid movement among the hairs or feathers of their hosts. Each leg (Fig. 214) consists of a coxa, trochanter, femur, tibia, and tarsus, the latter composed of five segments. The last pair of legs is usually larger than the others and functions extremely well in the act of jumping.

The abdomen consists of at least ten segments, of which nine can be readily recognized. The last three segments are greatly modified for sexual purposes and, in the male, present the most striking and bizarre structures (Fig. 214). In the female the abdomen appears ovoid in shape and ends rather bluntly. Within the abdomen of the female can be seen the spermatheca, a rather striking, somewhat pigmented organ (Fig. 223). This organ varies greatly in shape in different species and is used extensively for taxonomic purposes. The terga and sterna of the various segments can be easily recognized. On the posterior margin of the seventh segment is located the antepygidial bristle or, in many species, bristles (Fig. 214, Psp). In the figure it consists of three macrochaetae, one on each side of the middle one that projects backwards. Back of the eighth segment is located a small, more or less heart-shaped area, the pygidium (Pg), part of the tergum of the tenth segment. Its function is not known. It bears many setae arising from clear, circular areas. It probably is sensory in function. Below the pygidium, arising from a slight elevation, is a group of rather stout setae, the anal stylets. The spiracles normally number ten, two on the thorax and eight on the abdomen.[1]

BIONOMICS OF FLEAS

LIFE HISTORY: The eggs are ovoid in shape and white or creamy white in color. They are deposited either in the nest, burrow, or similar abode of the host or laid on the host while the females are feeding. They are not glued to the host but are laid among the hairs or feathers, whence they fall off commonly in the sleeping places or in the haunts most frequented by their hosts. *Pulex irritans,* the human flea, is said to lay most of its eggs when free from its host. As a result the haunts, resting places, burrows, and nests become heavily infested with the eggs and larvae, and the newly emerging adults find ready access to their favorite hosts.



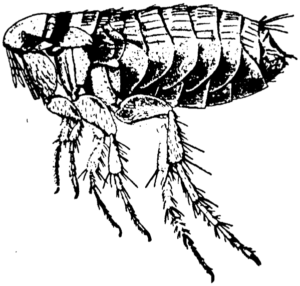


Fig. 216 (*left*). The common rat flea, *Nosopsyllus fasciatus.* Larva above and pupa below. (After Bishopp.)

Fig. 217 (*right*). Adult female of *Nosopsyllus fasciatus.* (After Bishopp.)

The eggs hatch, depending on moisture and temperature, in from 2 to 12 days. The young larvae are minute, active, elongated, legless, and eyeless creatures. They move about actively in the dust and debris in or near the nest of the host. Development is very rapid provided there is an abundance of food and the temperature and moisture conditions are favorable. In the human flea the larval period may be as short as nine days or greatly prolonged; in the dog flea as short as seven days; and in other fleas the larval period varies widely (see Table 9). The larvae, when mature (Fig. 216), are usually less than one-fifth of an inch in length. They are slender and each segment is provided with a number of bristles that assist in crawling. The head is distinct, the mouth parts are of the biting type, and a pair of slender antennae are present. The tip of the abdomen is provided with a pair of fleshy fingers, which aid in larval movements.

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[1] For a full and detailed discussion of the external anatomy of fleas, consult Snodgrass (1946).

The larval food consists of particles of organic matter present in the dust and dirt in which they live. Probably the most important source of food is the dried particles of blood voided by the adult fleas, which frequently fall where the larvae are feeding.

When mature the larvae spin silken cocoons to which particles of dirt usually adhere (Fig. 216). Within the cocoon molting takes place to form the pupal stage. The pupal period varies widely, from a few days (7) to nearly a year, depending on a variety of circumstances. The length of the life cycles of various species of fleas, especially of those of importance to man, is shown in Table 9 (from Bishopp, 1915).

Table 9. Life cycle of fleas in different countries.

Country and species	Length of egg stage	Length of larval stage	Length of cocoon stage	Complete life cycle
	days	*days*	*days*	*weeks*
UNITED STATES				
Atlantic coast				
Ctenocephalides canis (dog flea)	2–4	8–24	5–7	2–4
Nosopsyllus fasciatus * (rat flea)	6	13	18	37 days
Pacific coast				
Pulex irritans (human flea)	7–9	28–32	30–34	9–11
Nosopsyllus fasciatus	5–6	24–27	24–26	7–8
Xenopsylla cheopis (Oriental rat flea)	9–13	32–34	25–30	9–11
Oropsylla montana (ground squirrel flea)	7–8	26–28	24–27	8–9
EUROPE				*days*
Pulex irritans	4–12	8–100	6–220	19–264
Ctenocephalides canis	8–14	12–142	10–354	35–366
Nosopsyllus fasciatus	5–14	12–114	3–450	20–467
Xenopsylla cheopis	10 or less	14–84	9–191	31–256
INDIA				
Xenopsylla cheopis	2	7	7–14	21–22
AUSTRALIA				*weeks*
Pulex irritans	6	12	14	4–6

* At Ithaca, New York (unpublished thesis by Stanford).

BREEDING PLACES: Fleas breed in a great variety of places when the conditions of moisture and temperature are right and food is available. In houses they are found in the cracks and crevices of the flooring, under matting and carpets, and very frequently in the dust and debris in cellars, especially if cats and dogs are kept as pets and allowed to sleep in the cellar. Rat fleas breed in granaries, barns, warehouses, basements, chicken houses, and sheds. The young fleas may be found among the straw, sacking, rubbish, and other waste about and in buildings frequented by rats. Fleas have been found breeding in abundance under corncribs and other buildings where cats, dogs, chickens, and other animals rest during the heat of the day. Out of doors both the human flea and cat and dog fleas have been found breeding in lawns, particularly near buildings or under the shade of shrubbery where animal or vegetable matter is present in considerable amounts. The writer has seen lawns at Ithaca heavily infested with the cat flea and also garbage dumps where fleas were present in large numbers.

HABITS OF THE ADULTS

The adults are only periodic parasites on their hosts, coming to them primarily for food. Fleas feed at frequent intervals, usually at least once a day and sometimes much oftener. The frequent biting is due to the constant disturbance, the fleas not being allowed to complete their meal at one biting. Also fleas will feed to repletion and still continue to feed, passing almost unaltered blood per anum. Blood appears to be essential for the production of eggs. Fleas readily pass from host to host but the principal means of spread is by their hosts and through the scattering of their eggs as their hosts migrate from place to place. Fleas are famous for their powers of jumping but such powers are greatly exaggerated in the minds of people. Mitzmain found that the human flea could make a horizontal jump of at most 13 inches; the maximum vertical jump did not reach 8 inches; with other species of fleas the jumping powers are apparently much less.

Fleas are comparatively long-lived. In rather cool, humid climates the length of life is much longer than in dry, hot climates. Bacot (1914), in a most elaborate series of experiments, showed that the maximum length of life in various species was as follows:

	Fed	*Unfed*
Pulex irritans (the human fleas)	513 days	125 days
Nosopsyllus fasciatus (the rat flea)	106 days	95 days
Xenopsylla cheopis (Indian rat flea)	100 days	38 days
Ctenocephalides canis (dog flea)	234 days	58 days
Ceratophyllus gallinae (hen flea)	354 days	127 days

In California, Mitzmain records that the common rat flea lived for 160 days, the Oriental rat flea for 49 days, and the common ground squirrel flea, *Oropsylla* (*Diamanus*) *montana* for 64 days when fed frequently. In warm climates the longevity of unfed fleas is comparatively short. On the basis of his experiments, Bacot (1914) concludes that active adults in favorable situations, and when no hosts are available for considerable periods, can survive for the following periods:

Nosopsyllus fasciatus	22 months
Pulex irritans	19 months
Xenopsylla cheopis	10 months
Ctenocephalides canis	18 months

These long periods of survival may account for the presence of fleas in houses, camps, resorts, and similar places that have been unoccupied for months or even a year or more.

The reproductive capacity of fleas varies widely, though comparatively few exact observations have been made on this point. Bacot records the maximum number of eggs laid by a single female of *Pulex irritans* over a period of 196 days as 448, of which 115 were fertile.

CLASSIFICATION OF FLEAS

The order Siphonaptera contains probably over 1200 species from the world, and new species are being described every year. The order is divided into five or six families and far too many subfamilies and genera. The following abbreviated key will be of aid in placing the species that are of importance to man. (For more complete keys consult Ewing and Fox, 1943; Fox, 1940; Hubbard, 1947; and the extensive works of Jordan and Rothschild.)

KEYS TO THE FAMILIES OF SIPHONAPTERA

(And the More Important North American Species Associated with Man) [2]

1. Thorax greatly reduced; the thoracic terga taken together shorter than the first abdominal tergum; gravid females greatly distended (Fig. 218) .... *Hectopsyllidae* 2

   Thorax not greatly reduced; the thoracic terga taken together normally much longer than the first abdominal tergum (Fig. 221) 3

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[2] This key will place species in their families. Under each family only those species associated with man in North America and with plague transmission are given. The identification of fleas is difficult and specialists should be consulted for most identifications.

2. Coxa of third leg with a patch of spinelets on inner surface; abdominal segments 2 and 3 with spiracles. The sticktight flea (Fig. 220) .... *Echidnophaga gallinacea* (Westwood)

Coxa of third leg without such a patch of spinelets; abdominal segments 2 and 3 of female without spiracles. Mainly restricted to warmer regions of world. The jigger or chigoe (Fig. 218) .. *Tunga penetrans* Linn.

3. The terga of abdomen typically with only one transverse row of setae (Fig. 214); groove between frons and occiput usually absent (the old suborder Integricipita, in part); eyes usually present .... *Pulicidae* 4

The terga of abdomen typically with more than one transverse row of setae; groove between frons and occiput frequently present. (The old suborder Fracticipita, in part) 9

4. Genal comb (ctenidium) absent (Fig. 222 *c*) 5

Genal comb present; pronotal comb present (Fig. 222 *a*) 7

5. Pronotal comb (ctenidium) absent (Fig. 222 *c*) 6

Pronotal comb present. A typical ground squirrel flea (Fig. 222 *g*) .... *Hoplopsyllus anomalus* Baker

6. Pleuron of second thoracic segment (mesosternite of authors, Fig. 214 Pl) divided by a stout, vertical, rodlike thickening. The oriental rat flea .... *Xenopsylla cheopis* (Roth.)

Pleuron not so divided. The human flea .... *Pulex irritans* Linn.

7. Teeth of the genal comb straight, blunt, black spines and arranged nearly vertically (Fig. 222 *j*). Hosts rabbits and hares of North America .... *Cediopsylla simplex* (Baker)

Teeth of genal comb curved, sharp spines (7 to 8) and arranged nearly parallel to long axis of flea (Fig. 222 *a*) .... *Ctenocephalides* 8

8. Frons high and well rounded; first two spines of genal comb shorter than the others (Fig. 222 *b*). The dog flea .... *C. canis* (Curtis)

Frons low, flat, and somewhat pointed, all spines of genal comb of about the same length (Fig. 222 *a*). The cat flea .... *C. felis* (Bouché)

9. Head somewhat elongated, ventral flaps present (2 or 3) on each side near to fronto-genal angle (Fig. 222 *i*). Parasitic on bats .... *Ischnopsyllidae*

Head not elongated; ventral flaps absent; not parasitic on bats 10

10. Genal comb absent; combs on the abdominal terga frequently present. Includes the family Ceratophyllidae of authors .... *Dolichopsyllidae* 11

Genal comb present; combs on the abdominal terga frequently present .... *Hystrichopsyllidae* 12

11. Pronotal comb of 12 or more spines on each side. The chicken flea .... *Ceratophyllus gallinae* (Schrank)

Pronotal comb of less than 12 spines on each side (Fig. 222 *d*); movable finger of clasper of male short, broad, flattened, and without black spinifrons, only spines. The common rat flea ....*Nosopsyllus fasciatus* (Bosc.)

As above except the movable finger of clasper is elongate, sword-shaped. Hosts restricted to species of ground squirrels (*Citellus* spp.) of the western United States east to Idaho. Considered an important vector of plague among its hosts (Fig. 222 *e*) .... *Oropsylla* (*Diamanus*) *montana* (Baker)

12. Genal comb consists of three sharp teeth directed backward. A common species on rabbits, mice, moles and other small mammals in the eastern United States .... *Ctenophthalmus pseudargyrtes* Baker

Genal comb of four teeth directed backwards, blunt (Fig. 222 *h*). A common species on mice and rats .... *Leptopsylla segnis* (Schön.)

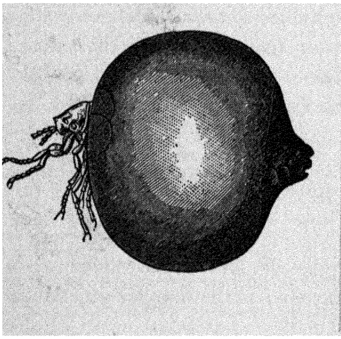
IMPORTANT SPECIES

The classification of fleas into families has not been accomplished in a very satisfactory manner, as illustrated by the preceding key. In the following brief account the species are placed, as far as possible, in the families generally accepted by taxonomists.

THE FAMILY HECTOPSYLLIDAE

The most important flea belonging to this family is *Tunga penetrans* Linn., the jigger or sand flea (the true chigger is a mite, *Eutrombicula* spp., see pp. 106–111). It is one of the most annoying pests of tropical and subtropical countries, where it frequently occurs in immense numbers. It is native to the New World and was introduced into the continent of Africa late in the nineteenth century. Since then it has spread to India and parts of the Far East. In America it occurs in Florida, the West Indies, Mexico, and Central and South America.

The jigger is the smallest flea known, measuring only about 1 mm. in length. The adults are fond of warmth and drought and may be found in immense numbers in dry dust in and about human habitations. The males and virgin females attack a wide range of hosts, practically all warm-blooded animals. Man and pigs appear to be favored hosts, though cats, dogs, and rats are readily attacked. When the female is fertilized, she remains on the host and burrows into the skin. Her favorite points of attack are between the toes, under the toenails, in tender parts of the feet, and in similar places. Here, nourished by the host's blood, the eggs begin to develop. The abdomen now swells up almost to the size of a pea (Fig. 218), the posterior end barely reaching beyond the swelling of the host's skin and forming a plug for the hole. The eggs mature and are expelled through the tip of the abdomen. When all her eggs are laid, the female shrivels up and drops out or is expelled by ulceration. The eggs drop to the ground and, if they fall in suitable situations, hatch and the larvae mature. Hicks (1930) states that, under experimental conditions, the eggs hatch in from three to four days. He reared the larvae on dried insects' tissues saturated with blood. He found the entire life cycle took about 17 days. Faust and Maxwell (1930) report an interesting case of a patient in New Orleans who became infected from sitting on sisal hemp that had just been imported from Yucatan. The infection occurred about the pubic and inguinal regions and the lower right quadrant of the abdomen. They found large numbers (several hundreds) of the larvae, in all stages of development, in scrapings from the infested skin. This finding is unique as it is probably the first authentic record of larval development in the skin of a host.



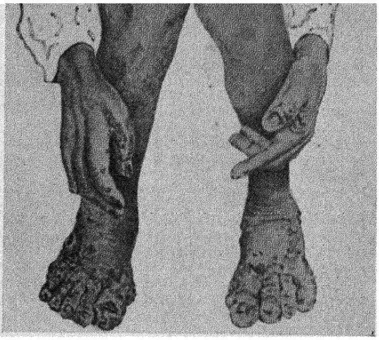


Fig. 218 (*left*). The jigger flea, *Tunga penetrans.* Gravid female. (From Ewing.)

Fig. 219 (*right*). Lesions of hands and feet due to the jigger flea, *Tunga penetrans.* (Photograph by Daniels, from Manson-Bahr, *Tropical Diseases,* by permission of Wm. Wood and Company.)

The wounds made by the burrowing females cause itchiness and inflammation and become very painful. As the females develop in size, the swellings grow larger and ulceration may follow, especially after the females have discharged all their eggs. These sores, especially on the feet (Fig. 219), may become secondarily infected, resulting in gangrene, tetanus, and other diseases.

Children playing barefooted near piggeries or on roadways or streets over which pigs are driven become heavily infected and frequently die from gas gangrene and tetanus. When the feet are badly infected, walking is impossible and Patton points out that in the East African campaign during World War I the troops suffered severely from this terrible pest.

The treatment for this flea when embedded in the tissues is not very satisfactory. Each flea can be removed under aseptic conditions by enlarging the entrance hole with a clean needle and carefully removing the entire flea. The wound should then be thoroughly sterilized and dressed. The proper prophylaxis is the wearing of boots or shoes with close-fitting leggings in regions where the flea is abundant; the housing of domestic animals as pigs and fowls away from human dwellings; the cleaning of yards and dwellings of dust, debris, and other refuse so as to reduce the breeding grounds; and forbidding the driving of infected animals over roads, streets, and other places frequented by barefooted children. Several other species of this genus are known: one, from China, in the ears of rats; one from Peru, and a few more from different parts of the world. They are not reported as attacking man.

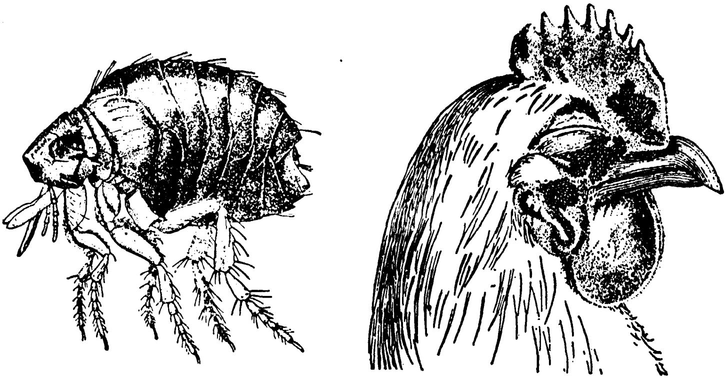


Fig. 220. Echidnophaga gallinacea. Left: The adult female. *Right:* The head of a rooster infested with this flea. (After Bishopp.)

The "sticktight" flea, *Echidnophaga gallinacea* (Fig. 220), is an important pest of poultry in most tropical and subtropical countries. It is very prevalent in the southern and southwestern parts of the United States and occurs as far north as New York, Minnesota, and Oregon. It is a small, dark-colored flea and, unlike its relatives, does not move about after it once has obtained a feeding ground but remains attached, with its mouth parts deeply embedded, for days or weeks. It is also gregarious and localizes in dense masses as on the heads of poultry and the ears of dogs or cats. Bishopp reports it as frequently attacking dogs, cats, rabbits, ducks, turkeys, and only occasionally man. It is not known to parasitize man to any extent, though children may become infested.

THE FAMILY PULICIDAE

HUMAN FLEA: *Pulex irritans* Linn. (Figs. 221,222 *c*) is known as the human flea. It occurs in practically every part of the earth frequented by man and man is its primary host. It also attacks badgers, skunks, dogs, squirrels, and other animals. It is said to be the predominant flea on the Pacific coast, where it is very annoying to man. It can be distinguished from the other common fleas by the characters given in the keys. This flea secretes itself in the cracks and crevices of houses, in floors, rugs, and bedding, coming out at night, like the bedbug, to attack its hosts. It breeds freely in all situations occupied by man and is extremely resistant to all adverse conditions. This flea may act as a vector of bubonic plague and should be regarded as a dangerous pest during an outbreak of the disease.

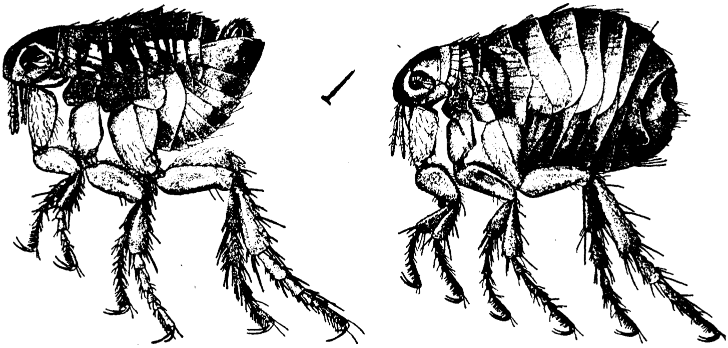


Fig. 221. Pulex irritans, the human flea. *Left:* Male. *Right:* Female. (After Bishopp.)

THE DOG AND CAT FLEAS: The dog and cat fleas (*Ctenocephalides canis* Curtis and *C. felis* Bouché) are practically cosmopolitan in their distribution. The cat flea (Fig. 222 *a*) is more abundant in temperate climates and is found as commonly on cats as dogs throughout the United States; in fact, it is the dominant flea of our domestic pets. The dog flea (Fig. 222 *b*) is said to be more prevalent in warm climates, though it is widely distributed

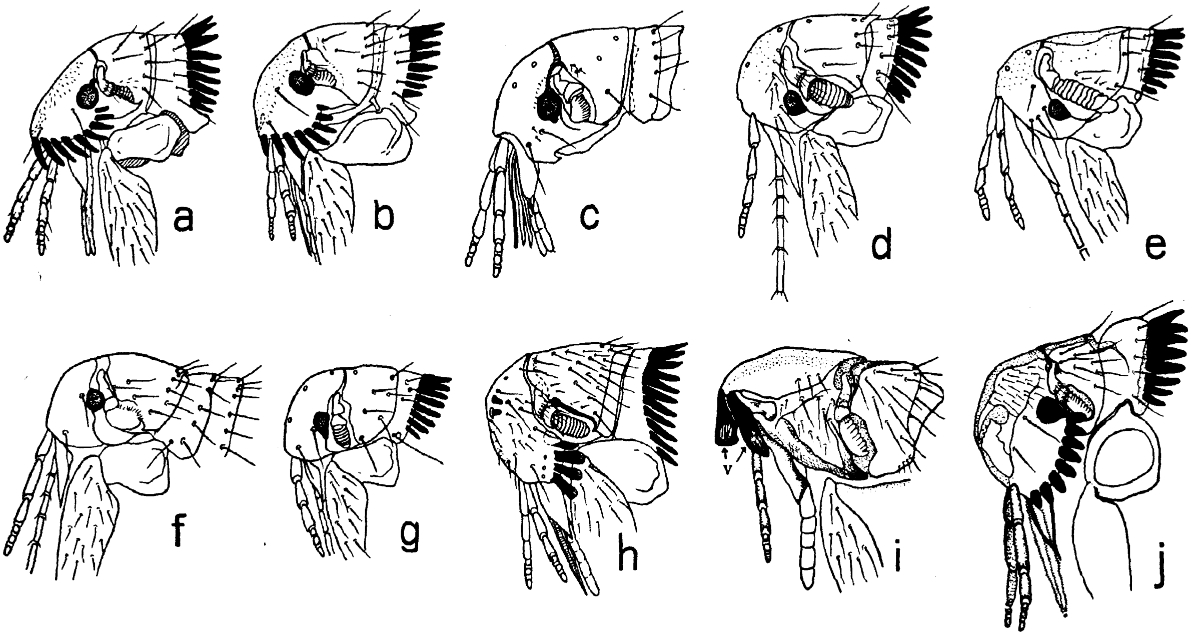


Fig. 222. Illustrations of fleas. (*a*) *Ctenocephalides felis.* (*b*) *C. Canis.* (*c*) *Pulex irritans.* (*d*) *Nosopsyllus fasciatus.* (*e*) *Oropsylla* (*Diamanus*) *montana.* (*f*) *Xenopsylla cheopis.* (*g*) *Hoplopsyllus anomalus.* (*h*) *Leptopsylla segnis.* (*i*) *Myodopsylla insignis.* (*j*) *Cediopsylla simplex.* V, ventral flaps. (Drawn by Miss Fernow.)

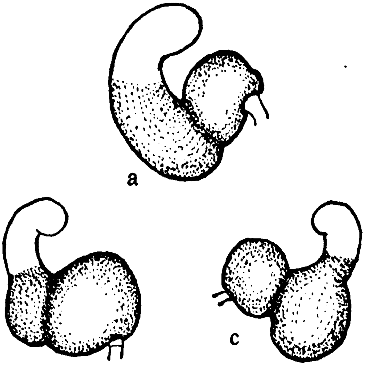
in temperate climates. The cat flea appears to have a wider range of hosts; however, both species readily bite man and have been taken from rats, skunks, and other mammals. The two species can be separated with difficulty, and the main differentiating character is the shape of the head—short and rounded in *canis,* long and pointed in *felis.* Both species can be readily separated from any other of our common fleas with similar habits by the two conspicuous combs, one on the head and the other on the pronotum. These two species are usually the common ones found in our houses and are very annoying on account of the avidity with which they bite many people. They sometimes occur in houses in enormous numbers, especially where cats and dogs are kept as pets and have their sleeping quarters in the rooms or cellar. These fleas usually lay their eggs on their hosts, and they drop off in showers when the animal shakes itself or they fall off in the sleeping quarters. Such enormous numbers of the cat flea have been reported as present in vacant houses that when occupied the residents could not remain. The writer has seen lawns in Ithaca so heavily infested with the cat flea that the inhabitants could scarcely move about without collecting large numbers of them. Here the fleas probably bred in moist, sandy areas occupied as sleeping quarters by stray dogs and cats or the domestic pets of the household.

ORIENTAL RAT FLEA: *Xenopsylla cheopis,* the Oriental rat flea (Fig. 222 *f*), is probably the most important species because it appears to be the principal vector of plague. Originally of African origin (Nile Valley), it has spread with its host, domestic rats, to all parts of the world. It is essentially a flea of warm climates and does not become permanently established in regions with long, freezing winters. In the United States it is present on the east, south, and west coasts, being the dominant flea in our southern ports. It is readily transported from port to port by ship rats, the black, roof, and Norwegian rats. In recent years this flea has been found in various parts of the interior of the country: Indiana (1925), Iowa (1934), Minnesota (1936), Tennessee (1940), and other states as Illinois, Ohio, New York, and Kansas. Though primarily a parasite of rats, it readily attacks man. Its relation to disease is discussed later.

Other important species are *X. astia* Roth., widely prevalent in the Orient and particularly in India; *X. brasiliense* Baker, an African species that is now widespread in southern India, Africa, and South America. These three species are primarily parasites of rats, mostly of the black rat (*Rattus rattus* and its varieties) and the brown rat, *Rattus norvegicus.* The three species can be distinguished most easily by the shape of the spermatheca (Fig. 223). Another species, *X. eridos,* is prevalent on the rodents of the South African veldt and is associated with endemic plague occurring there. Many other species belonging to this genus have been described.

OTHER RODENT FLEAS

Here belongs a group of fleas that are not placed in the Pulicidae but in other families. One of the most important species is *Nosopsyllus fasciatus* (Bosc.), the common rat flea (Figs. 217,222 *d*), which is widely distributed in all temperate climates. Its chief hosts are rats and mice. It requires a rather cool climate for its best development. In Ithaca, New York, the life cycle requires about 37 days (the fleas were reared in a warm room during the winter)—egg stage, 6 days; larva, 13 days; pupal period, 18 days. The larvae apparently require blood for their development and it is obtained from the fecal wastes of the adult fleas. This flea readily attacks man, is one of the important agents in maintaining plague among rats in nature and aids in the spread of plague among humans. *Oropsylla* (*Diamanus*) *montana* (Baker) (*acutus* Baker) is a common squirrel flea in the western United States and readily bites man. The larvae live on the dried pellets evacuated by the adults. The flea is of importance as it maintains plague infection among squirrels and is a potential transmitting agent to man. Other species are *O. silantiewi* Wagner of Mongolian marmots and *C. tesquorum* of ground squirrels of Asiatic Russia, both species being vectors of bubonic plague. *Leptopsylla segnis* is pri-



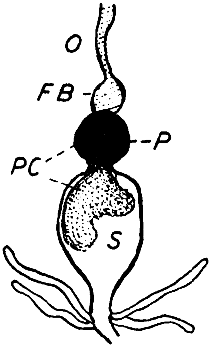


Fig. 223 (*left*). The spermatheca of *Xenopsylla* species. (*a*) *X. cheopis.* (*b*) *X. brasilense.* (*c*) *X. astia.* (Modified from Rothschild.)

Fig. 224 (*right*). Intestine of "blocked" flea. Note the distension of the esophagus with fresh blood. FB, fresh blood; O, esophagus; P, proventriculus; PC, culture of plague bacillus; S, stomach. (Redrawn from Bacot and Martin, *Journal of Hygiene.*)

marily a parasite of mice and rats, will occasionally attack man, and acts as a vector of plague. *Hoplopsyllus anomalus* Baker, a parasite of ground squirrels (*Citellus* spp.) in parts of California and Colorado, is known to be a vector of plague among these animals and it occasionally feeds on man. A number of other rodent fleas in various parts of the world are known to be of some importance in distributing plague among their hosts.

FLEAS IN RELATION TO MAN

Fleas have at least three important relations to man. These are:

1. The annoyance caused by their bites and the consequent irritation, especially to susceptible persons, and as direct causative agents (*Tunga penetrans*) of diseased conditions.
2. As intermediate hosts in the developmental cycle of parasitic helminths.
3. As vectors of disease among animals and as vectors of such diseases to man.

BITES

To most people the bites of fleas are extremely annoying. Some people seem to be immune, at least they claim they are never bitten, while others appear to be particularly susceptible and suffer tortures from even a single flea. When a flea bites it injects a certain amount of salivary secretion into the wound, which probably produces the irritation and itching. Ordinarily the irritation subsides in a short time, though in some cases it does not. The application of soothing lotions such as menthol and camphor, carbolated vaseline, or mild solutions of ammonia in water will often reduce the irritation.

INTERMEDIATE HOSTS OF PARASITIC HELMINTHS

Fleas serve as the intermediate hosts of certain tapeworms, some of which are occasionally parasitic in man. *Dipylidium caninum,* a common tapeworm of cats and dogs, has as its intermediate hosts the dog flea, *Ctenocephalides canis,* and the human flea, *Pulex irritans.* The eggs of the tapeworm are discharged by its host and are eaten by the larvae of the fleas. Within the larvae the eggs hatch and the embryos bore through the intestinal wall and remain within the body cavity without much change till after pupation and emergence of the adult fleas. Within the adults the cysticercoid stage develops, and new infections arise from swallowing infected fleas. Although over a hundred human infections of this tapeworm, mostly in children, have been recorded, it is not regarded as a serious parasite of man. Children obtain the fleas by playing with cats and dogs or drinking milk in which infected fleas have fallen.

Nosopsyllus fasciatus, Xenopsylla cheopis, and *Pulex irritans* (?) have been recorded as intermediate hosts of *Hymenolepis diminuta.* However, this tapeworm has numerous other insect intermediate hosts of much greater significance to man.

VECTORS OF DISEASE

PLAGUE: Fleas became of the greatest importance to man when it was finally demonstrated that rat fleas were the transmitters of bubonic plague, *Bacillus* (*Pasteurella*) *pestis,* by the British Plague Commission in India in 1906–1907. Plague ranks as one of the scourges of the human race, frequently occurring in epidemic form and killing large numbers of the population. Its place of origin does not seem to be definitely known, though Scott (1939) traces the disease to at least 300 B.C. (then a fatal disease in Libya, Egypt, and Syria) and probably back to the time of Homer (1184 B.C.). The first accurate account of a great epidemic was of the one that raged throughout Europe during the fourteenth century, killing off fully one-fourth of the entire population. From then till near the end of the seventeenth century it was almost constantly present in Europe. In 1665 the great plague of London took place and nearly 70,000 persons perished out of a total population of 460,000. Since then plague has appeared sporadically in parts of Europe, but it is said to have practically disappeared by the middle of the nineteenth century. Toward the end of the nineteenth century sporadic outbreaks occurred in certain European seaports; in 1894 it appeared at Hong Kong, one of the great shipping ports of the world, whence it spread by commerce to nearly all the seaports of the world. In 1896 plague appeared in India (Bombay), in 1898 in Egypt, in 1899 at Manila, the same year at Buenos Aires and Rio de Janeiro, in 1900 at San Francisco, and in 1914 in New Orleans. It has also become established in Mexico, Australia, and other parts of the world. Since plague appeared in India (1898), Heiser states that over 10,000,000 people have died, the annual death rate between 1898 and 1918 being 500,000. At the present time the death rate is probably less than 50,000 (as of 1935). The widespread introduction of the disease took place largely before our present knowledge of its epidemiology was known. However, there is constant danger of fresh introductions, and once the disease has become established in the rodent population, particularly in the wild rodent population, it is a strenuous and expensive fight to eliminate it. Witness the introduction into Java, where over 100,000 people perished in a few years. As a result of the widespread distribution of the disease and its establishment in native rats and other rodents, great endemic centers are now known to exist. The principal ones are in Manchuria, Mongolia, Central Asia, southeast

Russia, India, parts of Central and South Africa, parts of South America, and, in North America, a large area of the western United States extending from the Pacific coast east to the Dakotas, Kansas, and Oklahoma, south to Arizona and New Mexico, and north to British Columbia. In this extensive area naturally infected wild rodents occur, though human cases are rare.

Plague or black death is an acute, specific, febrile disease caused by *Pasteurella pestis;* it usually spreads to man from infected rats through the agency of fleas. The mortality both in man and rats is very high. It was not till 1894 that Yersin and Kitasato independently isolated the causative organism, *Pasteurella* (*Bacillus*) *pestis,* and the former established that the plaguelike disease in rats was identical with that in man. Simmonds in 1898 suggested that fleas were the transmitting agents, and Liston (1905) demonstrated the development of the bacilli in the gut of *Xenopsylla cheopis,* the Oriental rat flea. The British Plague Commission in India fully demonstrated the role fleas play in the dissemination of the disease (1906–1907). Finally, in 1914, Bacot and Martin definitely established the mechanism by which infected fleas transmit the disease from rodent to rodent and to man. Their observations were made on *Xenopsylla cheopis* and *Nosopsyllus fasciatus.* When the fleas imbibed blood containing *Pasteurella pestis,* definite brownish specks appeared in the stomach in a day or two. Later these increased in size as cultures of *P. pestis* and, in many cases, grew to such an extent as to occlude the stomach at its entrance. Further growth blocks the proventriculus (Fig. 224) and extends into the lower end of the esophagus (blocked fleas). While this growth is continuing, the fleas take blood, which furnishes an ideal cultural medium for the bacillus. Fleas when "blocked" and unable to pass fresh blood into the stomach are, nevertheless, persistent in their efforts to obtain blood. When they do the blood can only swell the esophagus, and on the cessation of the act of pumping (by the pharynx), some of the blood is forced back into the wound. Such blood is heavily loaded with the plague bacilli. Such infected (blocked) fleas live for a considerable time, persist in their efforts to feed, and are a constant menace to those on whom they attempt to obtain blood. Frequently the blocked food canal clears and the fleas can feed normally. Fortunately, blocked fleas are unable to withstand dry, hot weather and die off rapidly. In addition, feces from infected fleas are usually virulent, and human infection may occur from scarifying the skin with fecal wastes.

Plague is essentially a disease among rodents. Rats suffer from it, epizootics occurring among them frequently wherever plague is endemic or where it has recently been introduced. Man and other animals become infected through the agency of infected fleas. The spread of plague represents an etiological chain—the parasite, *Pasteurella pestis;* the susceptible hosts or reservoirs of the disease; and the vectors (fleas). In this case fleas are not true intermediate hosts but simply act as culture media and protective carriers of the bacillus. An outbreak of plague is practically always heralded by an epizootic among rats; then, the fleas finding their normal hosts missing, attack man. The maintenance and spread of plague is dependent on a great variety of rather complicated circumstances, which it does not seem wise to enter into here. The main points that may be stressed are the reservoirs of the disease (rodents) and the carriers (fleas). The principal reservoirs from which man is infected are rats—*Rattus rattus,* the black rat, and *Rattus norvegicus,* the brown rat, and their varieties. From these domestic to semidomestic rats, *Pasteurella pestis* may be carried to a great variety of wild rodents and thus a permanent reservoir becomes established. When this happens there is always constant danger of an epizootic among the wild rodents that may spread to the domestic rats and thence to man. The principal wild rodents that are known to serve as dangerous reservoirs are marmots (*Marmota bobac*) in Manchuria; and, in the United States, ground squirrels (*Citellus* spp.), mantled ground squirrels (*Citellus* spp.), marmots (*Marmota* spp.), prairie dogs (*Cynomys* spp.), chipmunks (*Eutamias* spp.), wood rats (*Neotoma* spp.), native mice (*Peromyscus* spp.), and some other animals. According to Eskey (1940), the main reservoirs in the United States are in ground squirrels, wood rats, and prairie dogs. In Central Asia and Russia ground squirrels (*Citellus* spp.) serve as reservoirs. The gerbiles, karroo rats, and the multimammate mouse (*Mastomys* sp.) are important in South Africa. Many other species have been reported from various parts of the world.

A large number of fleas has been shown experimentally to be vectors of plague. The following list, though not complete, gives the principal species and, as far as practicable, the principal regions where they are important vectors of the disease. Certain species, moreover, are known to be "good" or dangerous vectors in one region and "poor" vectors in others for reasons not clearly understood though generally given as climatic factors.

PRINCIPAL FLEA VECTORS OF PLAGUE

Xenopsylla cheopis Roth. (Oriental rat flea.) Throughout the world wherever plague is present and this flea occurs in abundance; mainly tropical and subtropical countries.

Xenopsylla astia Roth. Not regarded as a "dangerous" vector; said to be of importance in drier parts of India.

Xenopsylla brasiliense Baker. Experimentally it can carry plague but very little is known about its importance; reported an important vector in Kenya.

Xenopsylla eridos Roth. Regarded as important in the spread of rodent plague on the veldt of South Africa.

Nosopsyllus fasciatus Bosc. (Common rat flea.) Mainly important in temperate climates where it serves to spread plague among rodents and probably to man.

Oropsylla (Diamanus) montana Baker. (Squirrel flea.) Known to spread plague among ground squirrels and rodents in the western United States.

Oropsylla silantiewi (Wagner). Abundant on marmots of Mongolia and probably plays a role in the spread of plague.

Ceratophyllus tesquorum (*Wagner*). Spreads plague among ground squirrels in Asiatic Russia.

Pulex irritans Linn. Considered an important vector of plague during epidemics. Cosmopolitan.

Leptopsylla segnis Schön. Probably of little importance though it can spread plague among rats.

Hoplopsyllus anomalus Baker. Acts as vector among ground squirrels of the western United States.

Ctenocephalides canis Curtis. (The dog flea.) May be of importance during epidemics. Cosmopolitan.

Ctenocephalides felis Bouché. (The cat flea.) Plays a role similar to that of the dog flea. Cosmopolitan.

Ceratophyllus anisus Roth. Plague vector in the East Indies.

Stevalius ahalae Roth. Plague vector among field rats in Java.

SYLVATIC PLAGUE: In recent years plague as found in wild rodents has been designated as "sylvatic plague," and the plague endemic in domestic rodents as "murine plague." Sylvatic plague may, however, be transmitted to domestic rodents and thence to man or man may become infected from wild rodents if bitten by infected wild rodents. Unfortunately a great variety of wild rodents are known to serve as reservoirs of the plague organism, *Pasteurella pestis.* Among these rodents a large number of flea species has been proved experimentally capable of transmitting plague from animal to animal. This means that a constant reservoir of plague may be maintained from year to year and gradually spread over the entire country. In the United States wild rodents (ground squirrels) were first proved naturally infected in the region of San Francisco Bay in 1908. Since then infection in a great variety of native rodents has been demonstrated over the entire region west of the Rocky Mountains and east to South Dakota, Kansas, and Oklahoma and south to Arizona and New Mexico. The infection appears to be gradually spreading eastward, and the invasion of the great river valleys of the central states may prove very serious.

In order to restrict plague among wild rodents, it is necessary either to control such rodents or accurately to determine their fleas and to know which fleas are the important vectors. If such vectors are few in number, it might be possible gradually to eliminate such fleas. Unfortunately all evidence indicates that a large number of flea species are capable, experimentally, of transmitting plague among their hosts. Eskey and Haass (1940) state that nearly 50 species of fleas have been taken from wild rodents in the United States alone. Of this number they list 14 species capable of transmitting plague experimentally and 28 species that became infected when fed on infected guinea pigs.

Table 10. The important species of fleas incriminated as vectors or experimentally infected among native wild rodents in North America.

Species	Principal hosts	Distribution
xx*Hoplopsyllus anomalus* Baker	Ground squirrels (*Citellus* spp.)	Western United States
x*Malareus telchinum* (Roth.)	Deer mice and other wild mice	Western United States British Columbia
x*Monopsyllus ciliatus* (Baker)	Chipmunks	Western United States
x*Monopsyllus eumolpi* (Roth.)	Chipmunks	Western United States
o*Monopsyllus wagneri* (Baker)	Deer mice (*Peromyscus* spp.)	Western United States (east to Iowa); western Canada
o*Neopsyllus inopina* Roth.	Ground squirrels (*Citellus* spp.)	Western United States, British Columbia
xx*Opisocrostis bruneri* (Baker)	Ground squirrels	Great Plains west to Rocky Mountains, north to great plains of Canada
x*Opisocrostis hirsutus* (Baker)	Prairie dogs	Throughout the range of prairie dogs.
x*Opisocrostis labis* (J. and R.)	Ground squirrels	Western United States and western Canada
x*Opisocrostis tuberculatus* (Baker)	Squirrels	Western United States
xx*Orchopeas sexdentatus* (Baker) and varieties	Wood rats	Western United States (western Canada)
xx*Oropsylla (Diamanus) montana* Baker	Ground squirrels (*Citellus* spp.)	Western United States
o*Oropsylla idahoensis* (Baker)	Ground squirrels	Western United States
x*Oropsylla rupestris* (Jordan)	Ground squirrels	Western United States and western Canada

xx*Thrassis arizonensis* (Baker)	Ground squirrels	Western United States (southern part)
x*Thrassis a. acamantis* (Roth.)	Marmots	Northwestern United States; western Canada
x*Thrassis bacchi* (Roth.)	Ground squirrels	Alberta south through the Dakotas
x*Thrassis francisi* (Crox)	Ground squirrels	Utah, Nevada, Idaho
x*Thrassis h. howelli* (Jordan)	Woodchuck	California, Oregon, Nevada, Idaho
x*Thrassis pandora* Jellison	Ground squirrels (*Citellus* spp.)	Northwestern United States
o*Thrassis petiolatus* (Baker)	Ground squirrels	Northwestern United States; western Canada

xxImportant vectors. xExperimental transmission. oExperimentally infected.

ENDEMIC TYPHUS, MURINE TYPHUS OR FLEA TYPHUS: Dyer, Rumreich, and Badger (1931) demonstrated that fleas could transmit a mild typhuslike disease from wild rats to experimental animals. Since then this disease has been demonstrated to be caused by *Rickettsia mooseri;* the reservoir, rats and mice. Fleas (*Nosopsyllus fasciatus, Xenopsylla cheopis,* and others), the rat louse (*Polyplax spinulosa*), and the tropical rat mite (*Liponyssus bacoti*) maintain the reservoir in the wild hosts. Man becomes infected from the bites of infected fleas and mites, from infected flea feces rubbed into wounds, or from foods contaminated by infected rat urine (see pp. 98, 207).

CONTROL OF FLEAS

The problem of flea control involves a number of distinct measures. These may be roughly classified as (1) control of fleas on domestic pets and in the home; (2) control of fleas on poultry and domestic animals and in their living quarters; (3) control of fleas on rats and other wild rodents that are sources of plague; (4) prevention of the spread of plague by controlling the movement of infected rats and their fleas.

In private homes and public buildings the most essential and elementary principle in flea control, as with so many other insect pests, is strict cleanliness. Dirty corners, unclean rugs and carpets, dusty cracks and crevices, greasy kitchens, uncared-for and unkempt bathrooms and toilets, closets used as dumping places for dirty clothing, cellars littered with rubbish and filth, and other uncared-for places where the eggs of fleas, undisturbed, may hatch and the larvae obtain sufficient food and moisture serve as constant sources for flea multiplication. Cleanliness is the only remedy for such situations. Cats and dogs are the main sources for fleas in the home and public buildings. The destruction of stray cats and dogs and the maintenance of our pets in a clean condition with clean living quarters will practically assure the householder freedom from fleas.

In cases of home infestations the first procedure is the destruction of fleas on the dogs and cats and in their breeding places. If the house is infested, a thorough treatment with a 5 per cent DDT in oil (either in xylene, kerosene, or preferably anthracene) should be given. This should be applied to all infested rooms, spraying the floors and about two feet up the walls. The cellar should be cleaned and given a thorough spraying; if there is no cellar, the ground beneath the house should be sprayed. The fleas on the dogs and cats may be eliminated by dusting them with a 10 per cent DDT powder, placing the powder along the back and rubbing it into the hairs. All out-door premises such as kennels, storehouses, sheds, and the ground about them or where dogs and cats sleep should be sprayed. In all probability fleas can be controlled by simply dusting with a 10 per cent DDT powder. However, the powder is more annoying in the household and young children may swallow some of it. Its residual effect is not so lasting if the dust is swept up or vacuum cleaners are used. Effective treatments of houses can also be done by "fogging" by approved operators. In treating cats it is best not to use too much DDT as cats lick it and it may cause sickness.

In large establishments as public buildings, warehouses, and similar structures and in rural areas spraying or dusting with DDT should prove effective. This is much safer and the operation probably just as or more effective than fumigation with hydrocyanic acid gas. Furthermore in buildings infested with rats the spray treatment with 10 per cent DDT will usually reduce the rat flea population to a minimum. In rural areas experiments in spraying have given good results when the 10 per cent DDT spray was applied at such a rate as to leave 200 mg. per square foot. The residual action is lasting, usually for three or four months. Recently the work of Nicholson *et al.* (1948) demonstrated effective control of fleas, mosquitoes, and the tropical rat mite, ***Liponyssus bacoti,*** by using a water emulsion of DDT. The spray was prepared from a concentrate of 35 per cent DDT in xylene, and Triton X–155, diluted 1 part in 6 parts water. The spray was applied as for mosquito control: walls, ceilings, and about two feet of the floor next the walls were sprayed so as to leave a residue of 300 mg. per square foot. Rat holes, the cellars, and the ground beneath the buildings were also sprayed, using more material. All outbuildings, storage houses, and similar structures were also treated, care being taken to avoid contact with food. Such a treatment indicates effective control of both mosquitoes and fleas for several months and should be very effective in reducing endemic typhus and malaria.

Rats are being effectively controlled by the ratproofing of buildings and by the use, in experienced hands, of the newer poisons, 1080 and antu. It is interesting to note that a plague epidemic at Tumbes, Peru, was completely stopped in a short time by the use of a 10 per cent DDT powder and the poison 1080. The city of 10,000 persons was without a central water supply or a sewage system. Most of the houses were constructed of bamboo or wattle with mud floors. Thorough treatments (2 treatments) with the DDT powder almost completely eliminated the fleas, 1080 reduced the rat population, and plague was eliminated (Macchiavello, 1946).

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CHAPTER XIX

Poisonous and Urticating Arthropods

THE ill effects of the bites of various bloodsucking arthropods have already been indicated in the preceding pages. The irritation and the serious conditions not infrequently produced by such bites are due to the injection of the secretions of the salivary glands into the wounds. It has been shown that the secretions of the salivary glands of bloodsucking arthropods have various functions, such as 1 the prevention of coagulation of the blood (possess anticoagulins), and 2 may cause hemolysis (possess hemolysins), 3 produce paralysis (contain neurotoxins), or 4 act as direct irritants causing various reactions on the part of their hosts. (For accounts of such reactions see the discussions under the different species.) We need again to call attention to one important feature which is not stressed under each group of bloodsucking insects. When a bloodsucking insect bites there is always the possibility that the proboscis may be contaminated with pathogenic organisms. If such organisms become localized near the point of puncture or gain access to the blood stream, the results may be serious. It is always well to use some disinfectant as alcohol, tincture of iodine, or other antiseptic, and to press out blood, if possible, from the bites made by the insects. Dr. Walsh (1924) recommends an ointment of dimol well rubbed into the puncture and points out that Lord Carnarvon's illness and subsequent death arose from an insect's bite he received at the opening of Tutankhamen's tomb. The septic invasion took place at the point of puncture, spread with great rapidity, and death ensued from septic pneumonia. When going into any place where bloodsucking insects are abundant it is always well to be provided with several kinds of disinfectants and ointments. There remain to be briefly described the effects of poisonous arthropods, those species that normally do not act as bloodsucking parasites but occasionally bite or sting man and those that possess substances in their body covering of spines, hairs, etc., which, coming into contact with man, irritate his skin and often produce systemic and nervous disorders.

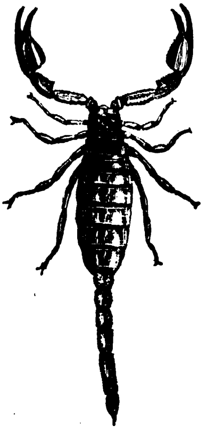
POISONING ARTHROPODS

Poisoning arthropods normally use their venom to kill or paralyze their prey or as weapons of defense. Man is bitten or stung when he accidentally or purposely intrudes upon them. Here may be included those arthropods that possess poison glands and utilize their secretions when they bite or sting. Such are the poisoning Arachnida, centipedes, millipedes, and certain stinging insects as bees, wasps, and stinging ants.

THE CLASS ARACHNIDA

THE ORDER SCORPIONIDA: Probably the most famous of the Arachnida are the scorpions (Fig. 225). Their characteristic form with their long, segmented, taillike abdomen ending in a bulbous sac and sting is familiar to everyone. Another feature is the long, somewhat formidable-looking pedipalpi that terminate in chelate claws similar to those of the lobster. Scorpions are found principally in warm countries, and certain species attain considerable size (up to eight inches in length) though most of them are small. They are nocturnal animals and of rapacious habits, feeding on spiders, insects, and other small animals. They seize them with their pedipalpi and sting them to death with the caudal sting. During the day they hide away under stones, wood, trash, or in small pits which they dig in the soil.

The poison glands of scorpions are located in a bulbouslike swelling in the last abdominal segment that terminates in a strongly curved, chitinous spine. The openings of the ducts from the poison glands are near the apex of the sting. Scorpions rarely sting man and then only under provocation. Though the sting is very painful, the poison rarely proves fatal to adults. The stings of the large tropical species often produce serious wounds and may cause alarming symptoms even in adults. In children under five years of age the stings of the larger species are serious, frequently causing convulsions, vomiting, and even death. Wilson (1904) records a considerable number of deaths among children each year at Omdurman (Sudan) from the effects of scorpion stings. Baerg (1929) gives an extended account of the famous scorpion, the "Durango" scorpion of Mexico (*Centruroides suffusus* Pocock). The sting of this scorpion is fatal to many children (one to seven years of age). He records 1608 deaths due to the sting of this scorpion in the city of Durango (population between 40,000 and 50,000) from 1890 to 1926. In 1927 forty deaths are recorded and seventeen for 1928. The effects of the poison are very rapid, death usually occurring within three hours; if the patient lives more than three hours recovery is practically assured, though death may occur six to eight hours after the sting. The stings of the scorpions appear to be more fatal during the hot season, April to July. The effects of the sting are very marked—immediate drowsiness, excessive salivation, tongue sluggish, distortion and severe contraction of the muscles of the lower jaw, while the temperature rises rapidly to 104° or 104.8° F.; there is scarcity of urine and usually a pronounced strabismus; there may be hemorrhages of the stomach, lungs, and intestines; convulsions come in waves and increase in severity for about one and one-half to two hours or, in fatal cases, until death.



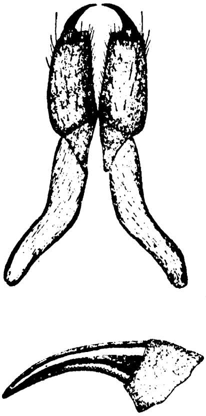


Fig. 225 (left). A scorpion.
Fig. 226 (right). Lactrodectus mactans. Upper: The chelicerae with the poison glands in place. *Lower:* A claw with the duct from the poison gland passing through it. (After Baerg, *Scientific Monthly.*)

The scorpion occurs in various parts of western Mexico and the southern part of Arizona but in no place so abundantly as in the city of Durango. Few deaths are recorded outside the city of Durango. In the city the scorpion frequents ruins, and Baerg found it almost exclusively under adobe bricks. It is also a common inhabitant of the houses and other buildings in the city.

Comstock (1948) records some twenty species of scorpions from the United States. The stings of our species are not considered serious though they may cause severe pain and slight systemic disorders. The stings may be treated with weak ammonia and this usually gives prompt relief. Ammonia may also be given internally. In cases of severe stings by the larger species prompt medical attention should be obtained. If not available a ligature should be applied proximad to the wound; the wound should be freely excised so as to cause a free flow of blood and washed frequently with a strong solution of potassium permanganate.

The principal species of scorpions in the United States which may sting man are *Isometrus maculatus* (occurs in southern Florida and California; widespread in subtropical and tropical countries; adults measure from two to three inches in length); *Centruroides* spp. (seven species found in the southern states and California); *Diplocentrus* spp. (two species, one in Florida and the other in Texas and California); *Vejovis* spp. (some seven species found in the Far West and Southwest); *Hadrurus hirsutus* (a very large, hairy species which occurs in the Southwest); and a few others.

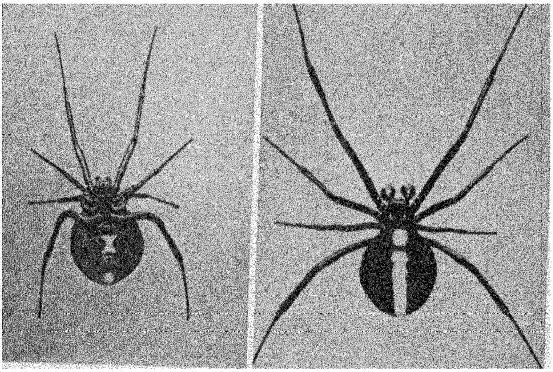


Fig. 227. Lactrodectus mactans, the black widow spider. *Left:* A ventral view of female to show the hourglass mark on the ventral surface of the abdomen. *Right:* Dorsal view of male. (After Baerg, *Scientific Monthly.*)

THE ORDER ARANEIDA: The true spiders differ from all other arachnids in having the abdomen unsegmented and attached to the cephalothorax by a short pedicel (Fig. 227). The four pairs of legs are attached to the cephalothorax. The mouth parts consist of a pair of chelicerae and a pair of leglike pedipalpi surrounding the mouth opening. Each chelicera (Fig. 226) consists of a large basal segment and a claw. The claw is hard, curved, pointed, and freely movable in one plane only. The claw is traversed by the duct of the poison gland (Fig. 226). Simple eyes (2 to 8) are usually present, though some species are blind.

Spiders are much feared by the average person. Such fears are usually quite unwarranted as spiders seldom bite man and then only under provocation.

However, spiders possess distinct poison glands, which open by means of ducts at the tips of the claws of the chelicerae (Fig. 226). All spiders are predaceous, the prey being seized by the chelicerae and crushed, and the injection of the poison either paralyzes or kills the victims.

THE POISON OF SPIDERS: All true spiders possess poison glands. The poison glands are two in number and are located in the anterior portion of the cephalothorax or in the basal segment of the chelicerae (tarantulas). The glands (Fig. 226) are more or less saclike and the lumen of the sac serves as a reservoir for the venom. Each gland discharges through a duct that opens near the tip of the claw of the chelicera of the corresponding side of the body (Fig. 3). The secretion of the glands is "an oily, translucent, lemon-yellow-colored liquid with an acid reaction and a hot, bitter taste." Kobert (1893) considers that there are two poisons present: (1) a toxin which causes local symptoms and is secreted by the glands; (2) a toxalbumin distributed throughout the body (not secreted by the glands) and producing general symptoms. In those spiders whose bites produce systemic disturbances it is believed that the latter poison greatly predominates.

Though the bites of spiders have long been considered dangerous, there is little positive evidence to support the view. Comstock (1948) concludes from long experience with spiders that there are none in the northern half of the United States that need to be feared. In the southern half the bites of species of *Latrodectus* are to be feared and probably those of certain species of tarantulas. In the North tropical tarantulas are frequently brought in on bunches of bananas but they rarely can be induced to bite.

LATRODECTUS SPP.: The hourglass spider or the black widow (*Latrodectus mactans* Fabr., (Fig. 227 ♂, ♀), is widely distributed in the southern half of the United States. It is a coal-black spider marked with red or yellow or both. Though the markings vary greatly, the most constant and distinguishing mark is the hourglass one on the ventral aspect of the abdomen (Fig. 227). The full-grown female's body measures about ½-inch in length or over all 1½ inches; the male 1⅛ inches over all. People generally recognize the venomous nature of the bite of this spider. Merriam (1910) records the Indians of California as dreading it and says, "All the tribes know that the spider is poisonous and some of them make use of the poison" (by rubbing the points of their arrows in the mashed bodies of the spiders). Riley and Howard (1889) describe the ill effects from the bite and report a fatal case. In all their reports the actual biting of the spider was not observed except in one case and in that case the specimen was lost. Kellogg (1915) describes an actual case. The spider (*Lactrodectus mactans,* female) bit the glans of the penis while the man was sitting on an outdoor closet. Ten minutes later the patient suffered from dizziness, weakness in the legs, and abdominal cramps. He walked a mile to the nearest physician and arrived suffering severely. The penis had greatly swollen, being fully three inches in diameter at the glans. The heartbeat was reduced to 40 per minute and the respiration was labored. Treatment consisted of hypodermic injections of strychnine 1/40 followed in ten minutes with nitroglycerine 1/100. The site of the bite was treated with potassium permanganate. The heartbeat went as low as 27 per minute but was restored to 45 after repeated injections of strychnine. At the end of three hours the strychnine treatment was stopped and 10 min. of brandy administered hypodermically every hour. At the end of nearly ten hours after the bite the heartbeat had risen to 55 per minute, and then a small dose of atropin and morphine was given to relieve the pain. The patient fell asleep and awoke next morning with a fine rash all over the body. The penis had returned to nearly normal size. Complete recovery took place in about four days.

Baerg (1923) describes the results of an induced bite of the same species on the inner surface of the basal joint of the third finger. Though he suffered considerable pain, was compelled to spend a day in bed, and had medical attention, yet the effects were not marked. The experimenter records that frequent hot baths and the keeping of the bitten hand in hot water were most efficacious in reducing the pain and restlessness.

Bogen (1926) reviews the reported cases due to the bites of this spider. He records some 150 cases from the United States and Canada. Fully two-thirds of them are from California and most of the victims were males who were bitten on the penis or adjacent parts while sitting on outdoor privies. He reports 12 deaths. He also records 15 cases at the Los Angeles General Hospital. All were males ranging from 2 to 65 years of age. Ten were bitten on the penis. The symptoms were acute pain, localized and general, profuse perspiration, restlessness, nausea, vomiting, labored breathing, and constipation. Treatment consisted of the administration of sedatives as morphine or codeine, bromides, etc., hot applications, such stimulants as ammonia, caffeine, and strychnine, and the use of purgatives as magnesium citrate or sulphate. Thorp and Woodson (1945) summarize the cases of spider bites in the United States, a total of 1291 cases (1726–1943) with 55 deaths.

Other species of *Latrodectus* occur in various parts of the world, especially in the tropics, and are generally regarded as dangerous. All of them are black or of a dark color marked with white, yellow, or red spots. *L. hasseltii* is widespread in the Philippines, New Zealand, and Australia. Its bites are regarded as serious.

TARANTULAS: Tarantulas are very large, hairy spiders (Fig. 228) belonging to the family Aviculariidae and commonly occur in the subtropics and tropics. On account of their size and fierce-looking appearance they are regarded by most people as very dangerous. There is little reason for this fear as there is no evidence that their bites produce any serious effects. Baerg (1923) induced a tarantula (*Eurypelma steindachneri*) to bite him on the finger but the effects were even less than those of an ordinary bee sting. *Seriocopelma communis* Cambr. is a common and much feared tarantula in Panama. Baerg (1929) reports this species capable of killing guinea pigs by its bite; on man its bite produces somewhat disturbing affects.

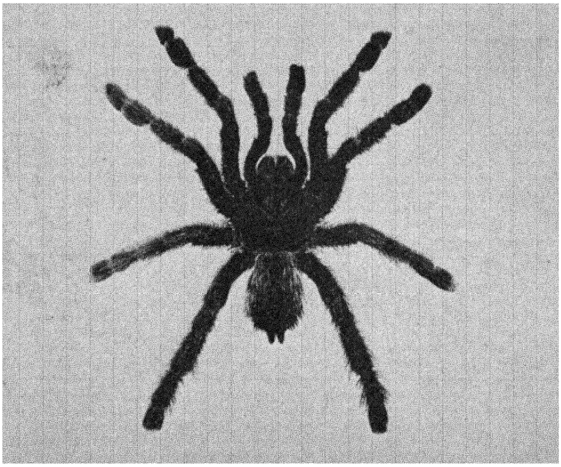


Fig. 228. A tarantula (*Avicularia* sp.)

The term tarantula was first applied to an European spider (*Lycosa tarentula*) which does not belong to this family. *Lycosa tarentula* is the famous spider whose bite was supposed to be the cause of a peculiar disease known as tarantism and prevalent in southern Europe during the Middle Ages. Warburton (1909) thus describes the supposed effects of this spider:

> The bite of the spider was supposed to induce a species of madness which found its expression—and its cure—in frantic and extravagant contortions of the body.

If the dance was not sufficiently frenzied, death ensued. In the case of survivors, the symptoms were said to recur on the anniversary of the bite. Particular descriptions of music were supposed to incite the patient to the excessive exertion necessary for his relief; hence the "Tarentella." In the Middle Ages epidemics of "tarantism" were of frequent occurrence, and spread with alarming rapidity. They were seizures of an hysterical character, analogous to the ancient Bacchic dances, and quite unconnected with the venom of the spider from which they took their name. The condition of exaltation and frenzy was contagious, and would run through whole districts, with its subsequent relapse to a state of utter prostration and exhaustion. The evil reputation of the tarantula appears to have exceedingly little basis in fact.

THE CLASS CHILOPODA—THE CENTIPEDES

The centipedes (Fig. 229) are wormlike creatures with the head distinct and a pair of antennae with many joints (at least 14); the body consists of numerous fairly similar segments, each with a pair of legs. They are tracheate animals and are mostly terrestrial. The class is divided into a number of families and the species are quite common and abundant, especially in warm countries. They are all predaceous and prey upon small animals. They are active, swift-moving creatures and are found in dark places as under stones, logs, rubbish, and dried leaves.

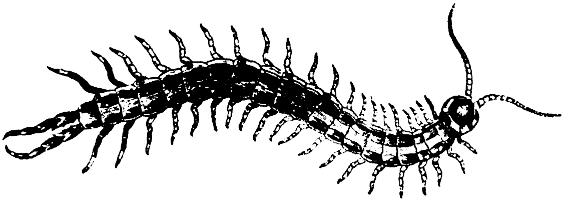


Fig. 229. Scolopendra obscura. (After Koch, *Die Myriapoda.*)

Centipedes are regarded as very dangerous by many people. They possess a pair of distinct poison glands that open near the tips of the fangs. The fangs are the modified legs of the first body segment and are located directly behind the mouth parts. Each fang is a curved, horny structure (Fig. 230) and the duct from the poison gland opens just behind the tip. Our larger species belong to the genera *Scolopendra, Lithobius,* and *Geophilus.* Some of the species attain a length of nearly seven inches. Cornwall (1916) investigated the poisonous properties of three Indian species (all in the family Scolopendridae) and found the toxic action of the venom relatively low. He considers the main function of the poison gland to be the secretion of digestive ferments rather than to furnish a lethal agent. Norman (1896) records *Scolopendra morsitans,* a species common in Texas, as capable of killing mice by its bite. Baerg (1924) made definite experiments on rats and himself with *Lithobius mordax* Koch, *Theatops spinicaudus* Wood, *Scolopendra heros* Gir., and *Scolopendra polymorpha* Wood. These species are more or less common in the southwestern United States. Herms (1923) records *S. heros* as common in southern California and much feared by the people. Baerg's experiments consisted in having the centipedes bite rats, noting the effects, and then inducing them to bite him on the inside of his little finger. *Lithobius mordax* had no effect on rats and was unable to puncture the skin of Baerg's finger; *Theatops spinicaudus* produced no ill effects on rats, and though it bit his finger and injected poison, no ill effects could be noted; *Scolopendra heros* (a specimen over 5½ inches in length) caused some pain to the rat by its bite but the pain apparently disappeared in a few hours; on himself the bite produced slight pain with a little swelling, which disappeared in the course of a few hours; *Scolopendra polymorpha* (a specimen nearly 6 inches in length) bit the rat readily but caused little discomfort; on himself the effects were even less than those of the preceding species.

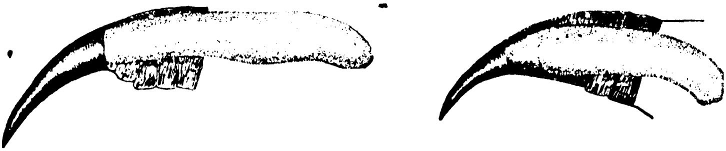


Fig. 230. Fangs of centipedes with poison glands in place. *Left: Scolopendra heros. Right: S. polymorpha.* (After Baerg, *Scientific Monthly.*)

Judging from the experiments of Cornwall and Baerg, it would appear that centipedes are practically harmless. However, some people might suffer severely from the same bites. Though centipedes should be avoided, there is no reason to fear them or dread their bites. When bitten by them the application of weak ammonia water and the use of antiseptics are recommended.

THE CLASS DIPLOPODA—THE MILLIPEDES

The millipedes or "thousand legs" are wormlike creatures (Fig. 231) and are all air-breathing, terrestrial arthropods. The entire body is more or less cylindrical. The head is distinct and the following four segments are generally referred to as the "thorax." The remaining segments constitute the abdomen and each segment usually bears two pairs of legs. The mouth parts are such that they do not possess poison glands and are of no value in inflicting wounds. However, many of the millipedes possess segmentally arranged glands that secrete a liquid that is an irritant to the skin. The liquid from these glands can be squeezed out or, in some cases, squirted with considerable force and to some distance. Loomis (1936, 1941) reports large millipedes (*Rhinocricus lethifer* and *R. latespargor*) in Haiti as squirting their fluids several inches, at least 24 to 36. Similar reports come from New Guinea and Africa, and the natives of many tropical countries regard these animals with fear. The fluid secreted is a strong skin irritant and if injected into the eyes may cause temporary or permanent blindness. Burtt (1947) gives an excellent summary and bibliography of injury from millipedes.

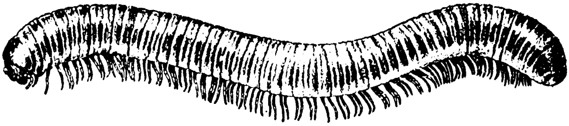


Fig. 231. A millipede, *Spirobolus marginatus.* (After Comstock.)

URTICATING INSECTS

Urticating insects are those whose body hairs (special types) when falling on or rubbed against the human skin cause local irritation, inflammation, or even systemic disturbances; and also those whose body fluids when placed on the skin cause blistering (blister beetles). The principal urticating insects are found among the caterpillars of the Lepidoptera (moths) and the beetles (Meloidae, or blister beetles).

LEPIDOPTERA: The chief urticating caterpillars belong to the following families: Megalopygidae, Eucleidae, Lymantriidae (Liparidae), Saturniidae, and Thaumetopoeidae. A few are recorded from the families Arctiidae, Noctuidae, and Nymphalidae (butterflies).

The urticating properties of these caterpillars are due to the possession of special hairs or spines that are supplied with a poison-gland cell. These hairs are hollow and filled with poison. When they come into contact with the skin, the fine barbed hairs penetrate or, if coarse, the poisonous substance spreads over the skin and produces the rash. According to Gilmer (1925), there are two distinct types of poison-gland hairs or setae. These he classifies as

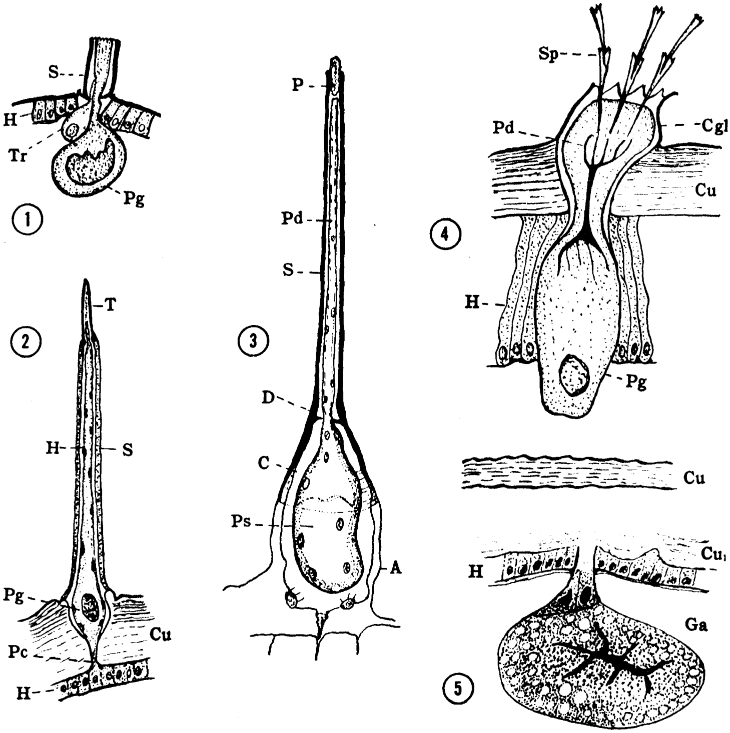


Fig. 232. Various types of hypodermal glands of insects, more particularly those that are protective. (*1*) Poison seta of white-marked tussock moth (*Hemerocampa leucostigma*). (2) Somewhat diagrammatic illustration of a poison spine of *Parasa hilarata* (caterpillar). (*3*) Somewhat diagrammatic illustration of poisonous spine of the puss caterpillar (*Megalopyge opercularis*). (*4*) Schematic illustration of a poison gland cell of the browntail moth (*Euproctis phaeorrhoea*). (5) Molting fluid gland from the cabbage worm caterpillar (*Pieris rapae*). A, cup of gland; C, collar of shaft; Cgl, cup of poison gland; Cu, cuticula; Cu_1, new cuticula forming; D, diaphragm at base of spine; Ga, molting gland; H, hypodermis; P, plug of pigment at end of poison spine; Pc, pore canal for the hypodermis; Pd, poison duct; Pg, poison gland cell; Ps, poison sac; S, spine; Sp, spicule hairs that are easily detached; T, tip of spine; Tr, trichogen cell. (*1* and *4* redrawn from Gilmer, 2 from Mills, *3* from Foot.)

the primitive hair type (Fig. 232 *1*) and the modified hair type (Fig. 232 2). The primitive hair type consists of a single seta, usually smaller and stiffer than the other body hairs of the caterpillar, and supplied with a gland cell that opens directly through a pore canal into the hollow of the seta. The seta contains the poisonous secretion or venomous cytoplasm of the gland cell. These setae retain their urticating properties long after they are shed by the caterpillar and their efficacy does not seem to be impaired by drying.

The modified hair type is found in many of the caterpillars of the Lymantriidae and some Thaumetopoeidae. The most striking type is that found in the caterpillars of the brown-tail moth (*Euproctis phaeorrhoea*). On the subdorsal tubercles of the caterpillars are found minute papillae or cuplike structures crowded together. In these cups are borne three to a dozen short spicule-like hairs of peculiar structure. These hairs consist of telescoped units, the fine point of one is inserted in the broad end of the part below it and the basal point is inserted in the "cup" of the gland (Fig. 232). These cups are continuous with the cuticle and each cup is connected with a large poison-gland cell located in the hypodermis. A true poison is secreted and passes out to the tips of the fine barbed hairs. As these minute hairs are shed they come in contact with the skin and penetrate it, causing the distinctive "brown-tail rash."

Another type is the so-called "spine type" (Fig. 232). This type is prevalent in the caterpillars of the Megalopygidae, Eucleidae, Saturniidae and Nymphalidae. Here the spine is usually quite large, the hollow interior is lined with a thin hypodermis, and the center is in direct communication with the poison-gland cell (Fig. 232). The tip of the spine can penetrate the skin, breaks off readily, and liberates some of the poisonous secretion. When numerous spines penetrate the skin there is produced a serious rash, often with systemic disturbances.

The nature of the poison found in these urticating hairs has not been determined. Foot believed it to be a true venom combined with protein vehicles. Gilmer does not think it a true protein as he failed to obtain any reaction with various protein reagents.

The general effects of these poison hairs vary according to the susceptibility of the individual. On some people the effects are very marked. Foot (1922) says, "The lesions produced by the sting of these genera [see list] vary from simple erythema, with burning or itching, to extensive inflammation, with the production of papules, vesicles, or bullae." Bishopp reports that *Megalopyge opercularis* sometimes occurs in such abundance as to cause an epidemic of dermatitis. At times the schools of San Antonio, Texas, have had to be closed because of the abundance of this caterpillar about the school grounds.

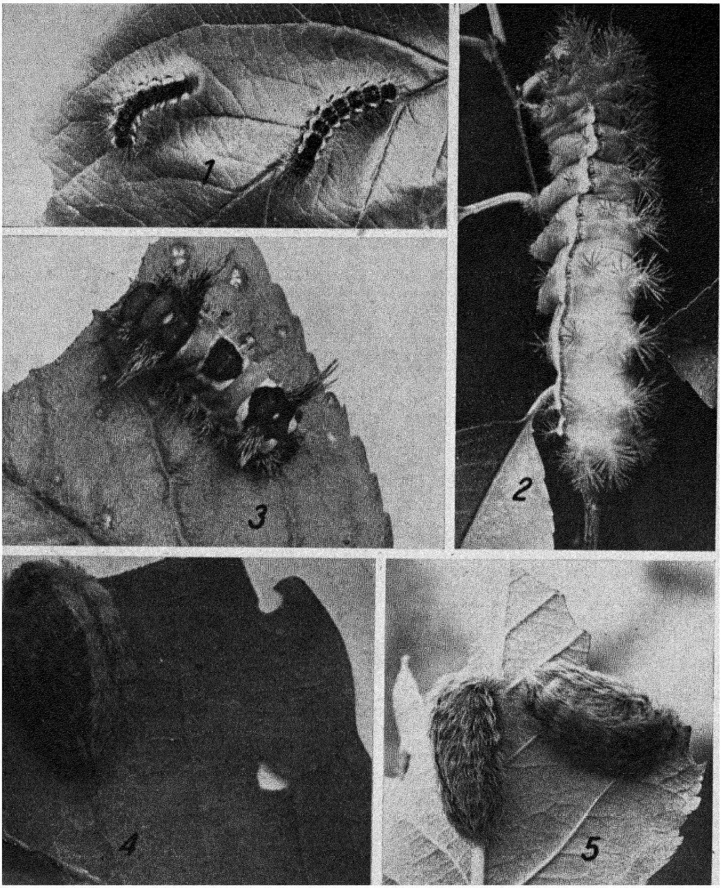


Fig. 233. Some urticating caterpillars. (*1*) *Euproctis phaeorrhoea,* browntail moth. (2) *Automeris io,* Io moth. (*3*) *Sibine stimulea,* saddle-back moth. (*4*) *Megalopyge opercularis,* puss caterpillar. (*5*) *Megalopyge crispata.* (Photographs by Slingerland.)

PRINCIPAL URTICATING CATERPILLARS

Megalopygidae:

Megalopyge crispata. Flannel moths. Northern United States.
Megalopyge opercularis. Puss caterpillars. Southern United States.
Megalopyge pyxidifera. Flannel moth. Southern United States.

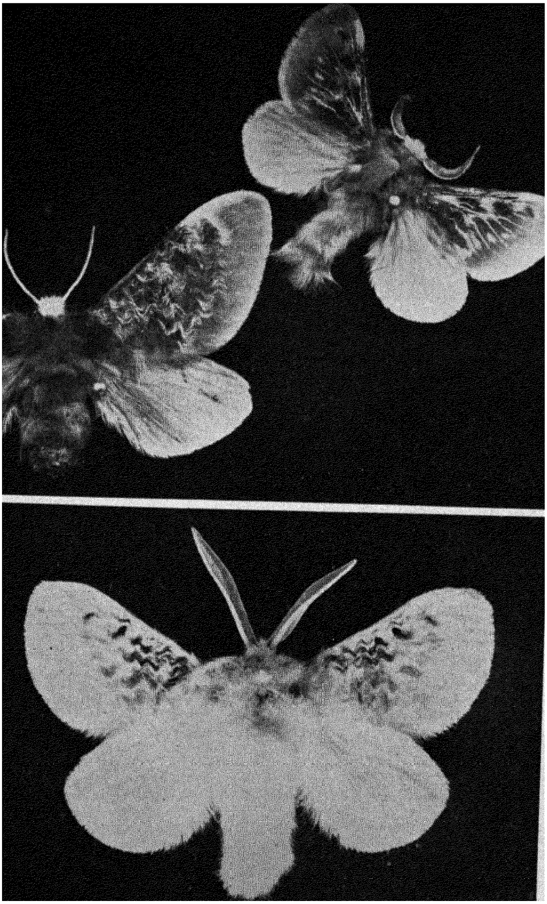


Fig. 234. Upper: Adults of *Megalopyge crispata.* Male and female. *Lower: M. opercularis.*

Norape ovina (*Cerama cretata*). United States.

As far as known all caterpillars of this family possess urticating hairs and the species are numerous in South America.

Eucleidae (Limacodidae):

Adoneta spinuloides. United States.

Parasa chloris. United States.
Parasa hilarata. Sino-Japanese area.
Parasa indetermina. United States.
Parasa latistriga. South Africa.
Phobetron pithicium. United States.
Sibine stimulea. Saddleback caterpillars. United States.
Numerous species in tropical regions of both hemispheres possess urticating properties of varying intensities.

Thaumetopoeidae:
Thaumetopoea processionea. Processionary caterpillar. Europe.
Several other species in Europe and North Africa.

Lymantriidae (Liparidae):
Euproctis chrysorrhoea. Gold-tail moth. Europe.
Euproctis flava. China.
Euproctis phaeorrhoea. Brown-tail moth. Europe and United States.
Hemerocampa leucostigma. White-marked tussock moth. North America.
Stilpnotia salicis. Satin moth. Europe and North America.
Probably many others of this family.

Arctiidae:
Euchaetias egle. United States.
Halysidota caryae. Hickory tiger moth. North America.
Probably a few others affect delicate skins.

Noctuidae:
Apatela populi and *Apatela oblinita.* United States.
Catocala sp. United States.
Effects from the larvae probably very insignificant except on the most delicate skins.

Saturniidae:
Automeris io. The Io moth. United States.
Automeris spp. Probably many species of the genus possess urticating hairs or spines.
Coloradia spp. Probably all species.
Hemileuca lucina. United States.
Hemileuca maia. The buck moth. United States.
Hemileuca oliviae and *Hemileuca nevadensis.* Western United States.
Hemileuca spp. Probably all species of the genus possess urticating hairs.
Pseudohazis eglanterina and *Pseudohazis hera.* Western United States.

Undoubtedly many other species in various parts of the world, particularly in tropical countries.

Nymphalidae:

Euvanessa antiopa. The mourning cloak. North America and Europe.
Vanessa io. Europe.

Very mild urticating properties, even to the most susceptible.

URTICATING (Vesicating) BEETLES: The principal urticating or vesicating beetles belong to the family Meloidae, or blister beetles. A few species are known from the Staphylinidae that possess urticating or blistering properties. In the Meloidae the urticating or blistering substance (cantharidin) is contained in the body fluids. Commercially it is extracted from the dried bodies of various species. The extract is used in medicine both as a blistering agent and internally in small doses as a diuretic and a stimulant to the urinary and reproductive organs.

Blister beetles frequently occur in vast numbers and are very destructive to foliage. When such beetles (Fig. 235) are handled, crushed against the skin, or in other ways come in contact with the body, there is produced a distinct dermatitis (vesicular). Treatment consists of pricking the blisters and covering with antiseptic dressings.

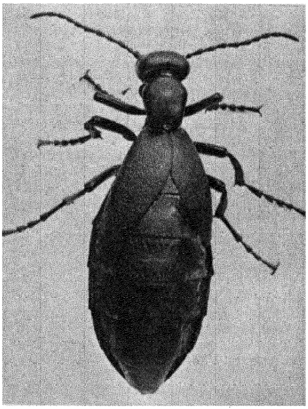


Fig. 235. Blister beetle (*Meloe* sp.)

In the Staphylinidae (rove beetles) practically only one genus, *Paederus,* is known to possess vesicating properties. The genus contains over two hundred species, widely distributed throughout the world. The beetles are small, the elytra are short; they have the habit of curling up the abdomen when disturbed. When handled roughly or crushed they produce typical blisters on the hands or body. Some of the more important species are *Paederus fuscipes* (Oriental region); *P. sabaeus* (tropical and South Africa); *P. cribripunctatus* (East Africa); *P. peregrinus* (Java); *P. amazonicus* (Brazil); *P. columbinus* (Brazil); and *P. irritans* (Ecuador). Gordon states that the blisters do not appear until a day or two after contact. The blisters are somewhat difficult to heal. Treatment is similar to that recommended for blister beetles. In all cases, blister beetles and rove beetles should be handled with care or avoided.

STINGING INSECTS

Stinging insects are provided with a sting, a modified ovipositor, which is connected with special poison glands. All stinging insects belong to the order Hymenoptera. The principal families that contain stinging forms are the Apidae (the honeybee, etc.); the Bombidae (bumblebees); the Vespidae (wasps and hornets); the Sphecidae (digger wasps); the Mutillidae (the velvet ants); the Formicidae (stinging ants); and probably a few others.

The worker honeybee possesses a very effective sting and an adequate supply of poison provided by two types of poison glands. When it stings the entire sting, the tip of the abdomen and poison glands are left attached to the wound. The muscles continue to contract, forcing the barbs deeper into the wound and discharging more poison. When stung, the first treatment is the immediate removal of the sting—not by seizing it and pulling it out (this only forces in more poison) but by pressing it out by means of the fingernail or a knife blade. Then bathe the parts with weak ammonia and treat with hot compresses. In some people, especially when they are stung over the eye, on the lips, the scrotum, etc., the effects may be very severe, as extensive swelling may develop, accompanied by great weakness, labored breathing, etc.; a physician should be consulted at once.

The stings of wasps, hornets, and bumblebees produce somewhat similar effects, and the treatment is the same as for the stings of the honeybee. There are many species of stinging ants, some of which possess very effective stings. Bequaert (1926) calls attention to the severity of the stings of a ponerine ant, *Paraponera clavata* Fabr. This ant, the so-called "tucandeira," occurs over an extensive area in Central and South America. They are very fierce ants, readily attacking when disturbed, and their stings are very severe.

Within the past few years attention has been called to the production of coryza and asthma by the hairs, scales, and the like, given off by various insects. Parlato (1929, 1930, 1932) has demonstrated that the hairs from caddis flies and the scales from moths and butterflies may be the cause of allergic coryza and asthma. This investigator prepared allergens suitable for diagnostic tests of individuals susceptible to such agents. Figley (1929) found four cases in which individuals suffered from asthma due to the inhalation of minute particles of the shed skins (windblown) of the subimago of mayflies. An extract was prepared for diagnosis and one case desensitized by the injection of allergen. Benson and Semenov (1930) studied bee allergens, not only the venom and the adhering pollen but also an intrinsic bee protein. Ellis and

Ahrens (1932) have found cases of hypersensitiveness due to air-borne bee allergens.

Many persons are very susceptible to insect bites and stings. Though some work has been done in attempts to immunize sensitive individuals, the results, so far, have not been very satisfactory. McKinley (1929) briefly summarizes the results of previous work. He has also attempted to immunize sensitive individuals against mosquito bites. Though he prepared potent extracts of the salivary glands (2000 glands of *Aedes aegypti*), he failed to produce any apparent immunity in sensitive individuals or even localized immunity in small skin areas by repeated injections of the extract. However, he observes that some results indicate that individuals after prolonged stay in association with *Aedes aegypti* become immune to its bites. The problem of immunizing or desensitizing individuals who are allergic to insect bites, stings, or cuticular products is one of considerable importance, and we may expect to witness increasing interest and progress in this particular line of work.

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CHAPTER XX

Collecting, Preserving, and Mounting Insects

TO THE average worker the collection and preservation of insects present many difficulties. The identification of insects can be undertaken only by specialists. No individual can hope to identify all the groups, not even those that are bloodsucking, and so must depend on the generosity of co-operating specialists. In order that insects can be identified it is essential that they be properly collected, prepared, and preserved.

COLLECTION

DIPTERA, COLEOPTERA, HEMIPTERA AND SIMILAR INSECTS: For these insects a collecting equipment is needed and should be of the simplest kind, easily handled and stored. Elaborate equipment may be purchased from dealers in natural history supplies, but this is not necessary. Of course the kind, amount, and variety of equipment will depend on the extent of the work the investigator intends to undertake. This brief outline is not intended for the specialist but for the beginner, the medical man, the public health worker, or others who may desire to carry on some entomological investigations. A collecting net is essential, and this may be a homemade affair or purchased. For most of our insects it can consist of a piece of wire, heavy brass or ordinary galvanized wire of sufficient weight, bent into a circle, some 10 to 12 inches in diameter, the ends of which are twisted about each other to form a handle or the ends may be carefully twisted about a small cylinder and thus form a more comfortable handle. Small muslin bags, about 1 to 1½ feet deep, are prepared, and one is sewed on the ring. The extra bags should be carried as reserves. For collecting aquatic forms, as the larvae of mosquitoes, black flies, and the like, a special, rather heavy net is required. In order to combine both the air net and water net, the writer uses a cane especially fitted with a brass tip (Fig. 236). Into the brass tip is inserted a stout screw which can be easily removed. When it has been removed, nets fitted on stout brass rings of various sizes (5 to 6 inches in diameter and about 5 inches deep for aquatic collecting; 10 to 12 inches in diameter and 15 to 18 inches deep for the air net) can be screwed in and collections made when desired. The air net is so made that it folds together when removed from the cane. By inserting the screw an excellent cane is available. Such an outfit can be prepared at almost any garage where mechanics are available. On a long collecting trip it is always advisable to have several collecting bags or one made of good material such as bolting silk. Bolting silk (the most suitable quality is No. 00), though expensive, makes the equipment quite permanent. Instead of using an aquatic net, collections can be made by using the common strainers (3 to 5 inches in diameter). The strainers may be tied to a rod and used from the shore or they may be used alone while wading. With the strainer a white enameled cup of about the same diameter as the strainer should always be at hand. After dipping or collecting, the strainer is placed over the cup nearly full of water, and any aquatic forms may easily be observed and collected.

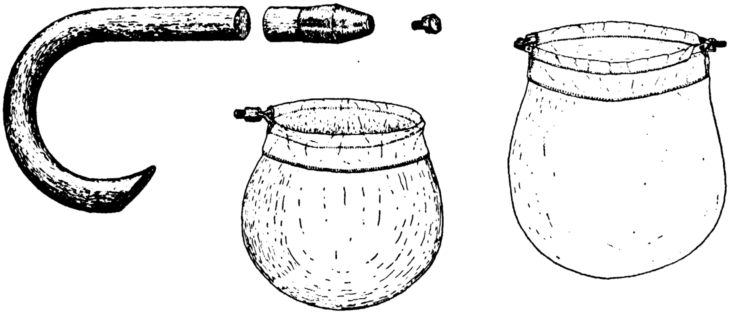
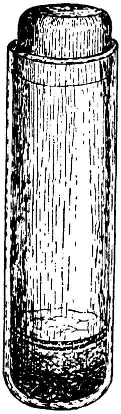


Fig. 236. Details of a cane collecting outfit used by the author. *Left:* The cane fitted with a brass cap; the end screw removed. *Center:* The small water net (about 5 inches deep and 5 inches in diameter). *Right:* The air net (about 16 inches deep). (After Matheson.)

KILLING BOTTLES: Collections may be made in small bottles and the specimens killed later in the laboratory or kept alive for future experimental work. Killing bottles can be made from heavy glass tubes (Fig. 237) or wide-mouthed bottles (Fig. 238). The chloroform bottle is probably the simplest type as it can be easily prepared and renewed. In the bottom of the tube or bottle place cut rubber bands or small pieces of rubber to the depth of an inch. Fill the bottle with chloroform to the top of the rubber. Place over this a small wad of cotton. On top of the cotton place several layers of blotting paper cut to fit the tube closely. The rubber will absorb the chloroform, and it is given up gradually so that such a bottle should last several days. Sodium or potassium cyanide makes effective killing bottles. Select a large-mouthed bottle or tube and place a small amount of sawdust in the bottom (about one-half inch). Over this place finely powdered sodium or potassium cyanide; then add another half-inch of sawdust. This should be well packed down, slightly moistened (a few drops of water), and covered with at least two layers of thick blotting paper cut to fit the bottle closely. Though the sawdust method is simple, most persons prefer plaster of Paris. Instead of the sawdust place a layer, about one-half inch, of dry plaster of Paris in the bottom of the bottle; over this add a layer of powdered (or small lumps will do) sodium or potassium cyanide. Pour over this a layer of plaster of Paris and water of the consistency of thick cream. Allow to set and when dry place over it two or three layers of heavy blotting paper, cut to fit the bottle. All killing bottles should be tightly corked. In order to prevent insects from becoming rubbed in the killing bottles it is always well to have small strips of soft paper placed in the bottles (Fig. 238).



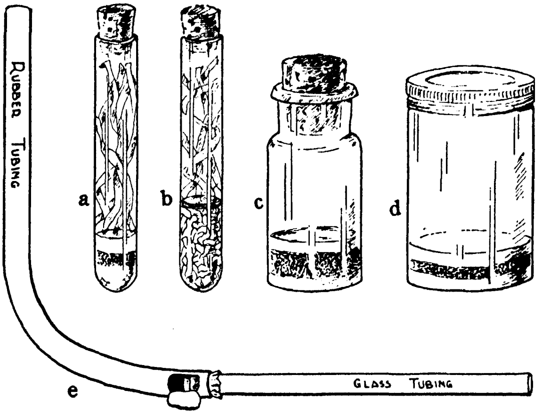


Fig. 237 (*left*). A simple chloroform bottle for collecting mosquitoes. (After Matheson.)

Fig. 238 (*right*). Collecting apparatus. (*a*), (*c*), and (*d*) Cyanide types of bottles. (*b*) Chloroform or ether bottle packed at base with cut rubber bands. (*e*) Aspirator tube (glass tubing with diameter of ¾-to-⅞ inch bore; place a piece of cheesecloth over end of glass tube before inserting it in the rubber tubing; this can be made any desirable size; very effective in collecting small flies such as mosquitoes.)

PRESERVATION AND MOUNTING

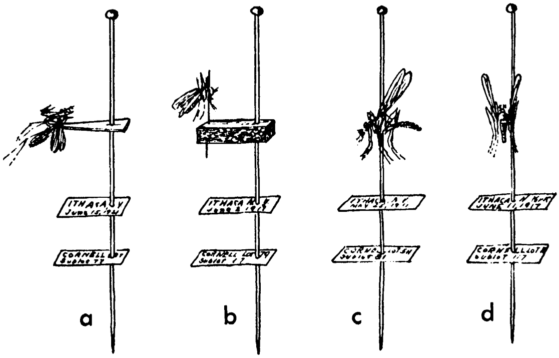
Adult insects can be preserved in alcohol (85 per cent), in formaldehyde (4 to 6 per cent), or in other preserving fluids. A fluid that is very satisfactory in preserving them in a soft and pliable condition is Kryger's solution. It is prepared as follows:

Acetic acid (33%)	62.5 cc.
Mercuric chloride solution (1 to 1000)	62.5 cc.
Glycerine	62.5 cc.
Alcohol (90 or 95%)	500.0 cc.
Distilled or ordinary water	312.5 cc.

In general, insects preserved in liquids are not easily identified and, in many cases, are impossible of identification. They may be preserved dry and carefully packed (not too many) in small pillboxes between layers of smooth sheets of cotton. By this method large numbers may be stored in small space. At any later time they can be prepared for pinning. It is always essential that full data on when, where, and how collected should be placed in the pillboxes.

The most satisfactory method, though tedious and time-consuming, is to pin material as soon as possible (within a few hours) after collecting. The size of pins to be used will vary with the size of the insects. For small insects such as mosquitoes and black flies, numbers 00, 0, and 1 are the most useful. The more minute and fragile flies should be pinned on *minuten Nadeln*. The various methods are illustrated in Fig. 239, with mosquitoes as examples. In pinning insects great care should be taken not to injure or destroy essential structures (as hairs, spines, scales, etc.) needed for identification. Large Diptera can be pinned directly through the thorax, preferably behind the transverse suture (if present); small Diptera can be pinned in a similar manner using very fine pins (No. 00), or they can be pinned through the side. In most cases it is preferable to pin first on *minuten Nadeln*, then insert the *minuten Nadeln* in a bit of pith, cork, or balsa wood; a stout pin is then driven through one side of the pith, and the specimen is ready for labeling (Fig. 239 *b*). Most workers keep a series of cork blocks with the *minuten Nadeln* driven through them, ready for pinning small insects. For Hemiptera, Hymenoptera, and some other large insects the pins are driven directly through the thorax. Coleoptera (beetles) should be pinned through the right elytra, the pin driven in a slanting fashion so that it emerges in the middle line on the ventral side. In pinning insects it is always a good practice to have sheets of thin cork or balsa wood at hand, and these serve as backgrounds on which to pin. In handling these fine pins good forceps should be available and, preferably, a suitable pinning forceps (Fig. 240). Exceptionally fine pinning forceps are the so-called "Cresson" type of entomological pliers manufactured by the Cleveland Dental Manufacturing Company.

After the insects are pinned each one should bear a label stating the place and time of collection, the collector's name, and any other pertinent data. The pinned material should be stored in insect cases, of which a great variety are on the market. Old cigar boxes lined with sheet cork, balsa wood, or even corrugated paper make excellent, temporary storage places. In the tropics and damp climates it is very difficult to keep pinned insects unless they are stored in tight, dry receptacles. Christophers recommends pinning small insects on short, fine pins on small sheets of cork, which are stored in vials, corked, and sealed with paraffin. Large insects can be pinned on the cork of the bottle, then the cork is inserted and sealed.



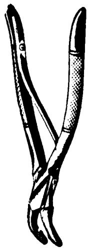


Fig. 239 (*left*). Various methods for mounting insects. (*a*) A mosquito pinned on a cardboard point. (*b*) Pinned on a *minuten Nadel*. (*c*) Pinned directly through the thorax. (*d*) Adhering to a drop of shellac on the side of the pin. (After Matheson.)

Fig. 240 (*right*). A type of pinning forceps (not the "Cresson" type).

When insects have been allowed to dry or have been stored, they must be relaxed before they can be pinned. The simplest type of relaxing jar is a large, deep petri dish. Place moistened filter or blotting paper on the bottom of the dish; over this add some soft nonabsorbent paper and then add the insects to be relaxed. Cover and allow to remain until the insects have become sufficiently soft that they can be pinned without danger of breakage. In this work avoid too much moisture and too many insects; be careful not to let the specimens remain too long in the moist chamber. It usually requires overnight or, in the case of large insects, a day or two. After they are relaxed, pin in the ordinary fashion.

Insect cases of all kinds, even the best manufactured, soon become infested with small museum pests that may destroy the dried bodies of the insects if care is not exercised. As a precaution always sprinkle naphthalene flakes in the bottoms of the cases, or store in small boxes in the cases, or use the prepared cones. "Globol," a patented product, is very effective and usually can be purchased from dealers in natural history supplies. When a collection becomes infested, fumigate with carbon disulphide, pouring the liquid directly in the cases or on cotton.

TICKS: Ticks (Ixodidae) may be collected from their hosts or in their hosts' habitats (the Argasidae). In searching an animal for ticks, exercise great care and examine all parts, particularly around and in the ears, back of and under the head, over the root of the tail, and inside the flanks. For most argasid ticks the host's habitat should be searched, examining all cracks and crevices, cracks in the soil, trash, and any other debris. In many cases, as with certain *Ornithodoros* species that bury themselves in the soil, collect the soil and sift it over white paper or cloth. This method is also effective when the habitats of burrowing animals are searched. Ticks should be removed from their hosts with care so as not to leave the capitulum deeply buried in the skin. Usually the application of chloroform or vaseline will induce the tick to withdraw its capitulum. Ticks should be preserved in alcohol (85 per cent) in small vials with the exact name of the host and time and place of collection. Never mix collections from different hosts.

OTHER MITES: In the case of permanent parasitic mites as *Sarcoptes* spp. and *Psoroptes* spp., the skin should be carefully scraped so as to reach the deeper parts. In the case of dead animals, parts of the diseased skin should be cut out and preserved. Always be sure to obtain sufficient material and preserve in alcohol (85 per cent). If it is desired to fix such material for histological purposes, place in the desired fixing fluid and follow the technique advised for the particular fixative. Patton strongly advises Bles's fluid as a general and effective fixing solution. It is prepared as follows:

70% alcohol	90 parts
Formalin (40% formaldehyde)	7 parts
Glacial acetic acid	3 parts

The greatest defect of this simple fluid is that it has to be prepared fresh for it rapidly deteriorates. Fix in it for 24 hours; decant and add fresh Bles's fluid;

leave for 24 hours; decant and preserve in 70 per cent alcohol, which should be changed to 85 per cent for permanent storage.

LICE: Sucking lice are always found on their hosts. The simplest method of removal is by means of a fine-toothed comb. Some infested hair should be cut off and preserved. Always cut the hair close to the skin so as to obtain the eggs (nits) and the nymphal stages. As lice usually remain and die with their host they can be collected from the preserved skins or carcasses. Remove them with a comb. When collecting living lice always keep them alive till they have digested their blood meal; it is much easier, then, to prepare them for study. Always preserve in alcohol (85 per cent).

FLEAS: Fleas are most easily obtained directly from their hosts. The collection of them is, at times, rather difficult. In places where they are abundant, as frequently in rat-infested buildings, basements, houses, etc., they can be collected in numbers by walking about with the legs wrapped with sticky flypaper. The fleas will be caught on the paper and can be removed later. For the chigoe, sand flea, or jigger, animals such as small pigs can be used as traps. The pigs are allowed to roam over the infested ground or they are held on their backs. Castellani and Chalmers state that the fleas readily collect on them and can be removed. Fleas normally leave their hosts at the time of the latter's death. When shooting birds, squirrels, small rodents, and the like for the purpose of collecting fleas, the dead animals should be placed promptly in tight paper bags and the bags securely tied. The fleas can be collected later. We have found that a most satisfactory method (devised by Dr. Wilson) for the collection of both biting lice and fleas is the prompt wrapping of the dead animal in a layer of cheap absorbent cotton; the fleas and biting lice leave the body of the host as soon as it is cold and become entangled in the fine cotton fibers. When the cotton is removed, the fleas and lice can be seen as small black spots and are easily collected. In fact, the cotton wrappings can be removed in a day or two, the dead animal thrown away, and the cottons, labeled and stored, can be searched at any convenient time. The fleas and lice will be found entangled in the cotton fibers. When burrows of rodents, birds' nests, etc., are searched for fleas, the simplest method is to collect a large amount of the earth and debris in and about the burrow (take the entire bird's nest), place in a tight paper or closely woven cotton sack, and examine later.

MOSQUITOES: Mosquitoes are difficult to collect in an ordinary air net because they become so rubbed when removing them tediously by hand. Most workers have to contend with the collecting of adult anophelines from buildings, under bridges and houses, from hollows in trees, etc. This work is time-consuming, especially if one collects with the ordinary cyanide bottle or attempts to capture the mosquitoes in individual bottles in order to obtain living specimens. Fig. 238 *e* illustrates what has been called an "exhaustor" or aspirator, which is easily constructed by anyone. With such an apparatus small insects such as mosquitoes can be readily collected and then blown out into cyanide jars or other containers if desired alive. Large numbers can be collected quickly when the technique is mastered.

THE PREPARATION OF SMALL INSECTS FOR STUDY

Most of the smaller, parasitic arthropods, as mites, lice, fleas, and larvae of all kinds, have to be prepared for microscopical examination. If detailed histological study is the objective, the methods of killing, fixing, and preserving the specimens in suitable media can be found in any of the numerous standard texts on histological technique.[1] To prepare for microscopic mounts the following method is probably the simplest and most easily carried out: If the specimens are in alcohol, formaldehyde, or other preservative, soak them in water for some time—a few hours to a day. Then place them in cold potassium hydroxide (10 per cent solution) and allow to remain until clear (usually a few hours to a day). If speed is essential, bring the cold potassium hydroxide slowly to the boiling point and boil only long enough to destroy the fleshy parts (this time can be learned only from experience, usually a few seconds to several minutes). With many insects as lice, fleas, and larvae, it is essential, in order to obtain good mounts, that the insects be punctured or cut with fine scissors or scalpel. The worker must learn his procedure from experience. (The writer punctures lice, fleas, and other insects before soaking them in potassium hydroxide, the punctures being so made that no injury is done to essential structures.) When suitably cleared, remove them from the potassium hydroxide and bring to a boil in a large amount of water. (The writer usually makes two changes of water, bringing to a boil each time.) The water removes the caustic potash and most of the remaining fleshy parts. If the insects or parts are small, transfer directly from the water to a slide and begin to dehydrate by starting with 50 or 70 per cent alcohol. Then run through the alcohols directly on the slide, allowing a few minutes (5 to 10) for each grade. Finally dehydrate in absolute alcohol[2] and mount in euparal. The writer finds euparal the best and, at the same time, the most permanent mounting media. This media clears in less than 24 hours and hardens in about the same time. If the specimens are thick or should not be compressed, the writer, instead of using the expensive hollow-ground slides, employs small pieces of crushed glass in the mounting media or narrow strips of thin or thick cardboard or microcells (the microcells are of glass or hard rubber; these can be purchased in almost any size and thickness). In handling small insects or parts of insects the writer always manipulates the parts, as legs and genitalia, while they are in the water on the slide. This is done under the binocular microscope and it is easy to spread out the parts while they are soft. Final arrangement (orientation of the specimens) is made in the euparal by means of minute needles (ordinary sewing needles, inserted in small wooden handles; the points being carefully ground on fine carborundum).

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[1] Patton recommends Bles's fluid as the best all-round fixing fluid.

[2] Dehydration can be done directly from water with cellosolve—from water to 50 per cent cellosolve for 5 to 10 minutes, then in pure cellosolve for the same time. Mount with euparal.

For larvae, especially mosquito larvae and others of about the same size, the writer finds the most satisfactory method is to kill in hot water (at about the boiling point), run through the alcohols (beginning with 30 per cent), dehydrate in absolute alcohol, and mount direct in euparal. The mosquito larvae are cut (either in the absolute alcohol or in euparal on the slide) just in front of the eighth segment. By this means a lateral view of the siphon and last two segments is obtainable. The entire larvae clear and make permanent mounts of great value (I have them in perfect condition after thirty years). Furthermore, in the euparal the finest hairs and spines stand out with the greatest clearness (due to the refractive index of the euparal).

Other methods are extensively used. Such are mounting in glycerine and glycerine jelly. Prepare material as outlined above but instead of dehydrating in the alcohols mount direct (from the water) in glycerine and seal the coverslip (various sealing media are on the market but the writer has found Bell's cement to answer best for every purpose). Mounting can also be done directly from water to glycerine jelly, though it is preferable to place the material first in 50 per cent glycerine (water and glycerine in equal parts). The glycerine jelly is placed on the slide, warmed till it melts, and the object placed in it and covered with a cover slip. Such mounts must be sealed. Unfortunately, all glycerine or glycerine jelly mounts dry out in time despite the most careful sealing. Canada balsam is probably the most extensively employed mounting medium, but the writer has not used it for the past thirty years, preferring euparal for all purposes, even for the finest histological preparations. If Canada balsam is desired, prepare as outlined for euparal but before mounting (after treatment with absolute alcohol) [3] clear in xylol, clove oil, or other clearing media and then mount in the balsam. Mounts made in euparal or balsam, especially if the parts are thick, should be watched as they dry, and small drops of the mounting media added at the side of the cover slip to avoid the development of extensive bubbles.

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[3] If absolute alcohol is not available it can easily be prepared from commercial 95 per cent. Dehydrate copper sulphate crystals by dry heat till they become a fine white powder.

For the larger larvae as those of the Muscidae it is better to preserve in alcohol (85 per cent) or Kryger's solution. For examination of the chitinous parts the entire larvae or parts of them can be boiled in caustic potash and then prepared and mounted in the usual manner.

DISSECTIONS OF INSECTS

The dissections of insects involve technique and skill. Carefull attention to details and the utilization of practically fresh or recently killed material are required. With the larger forms it is possible to make fair dissections with fixed material, but this is rarely advisable. As far as the average worker (exclusive of the laboratory worker, investigator, and teacher for whom this outline is not intended) is concerned, the most important technical problem is the dissection of mosquitoes for the examination of the salivary glands or stomach for infection with the malaria parasites. This dissection is comparatively easy and can be done by the average beginner with considerable assurance of success. Equipment need be only some small, sharp dissecting needles (ordinary sewing needles inserted in small wooden handles serve excellently; the larger needles can be made into microscopic scalpels by carefully grinding them on a fine stone under a hand lens or a binocular microscope); a few miscroscopic slides, pipettes, cover slips, saline solution (0.9 per cent), a dissecting microscope (not essential), and a compound microscope. If a binocular microscope (magnifications 24x to 72x) is available, the worker is relieved of many trials.

Kill the mosquito with chloroform (do not wet the mosquito) or, as the writer does, stupefy it with tobacco smoke in a small vial. Place the mosquito on a slide and cut off the wings and legs. Remove the scales and hairs with a small brush. With the mosquito on its side cut across the base of the thorax (Fig. 242) so that the abdomen is set free. Now transfer the abdomen to a clean slide in a drop of saline solution. With fine needles gradually cut the abdominal wall around the base of the seventh segment (Fig. 241), being careful not to penetrate too deeply into the body cavity and cut the alimentary canal. With this operation completed the alimentary canal can be removed by traction. Insert a needle in the dorsal part of the thorax and place another in

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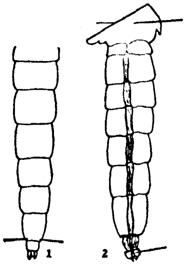
Place a varying amount in 95 per cent alcohol (depending on the quantity of absolute alcohol desired) and allow the copper sulphate to settle. In a few hours decant off the alcohol and it will be nearly 100 per cent pure.

the separated tip of the abdomen (Fig. 241). By gently pulling and relaxing, you can remove the alimentary canal with its attached organs. It can then be examined in saline solution under a cover slip or prepared in any way desired.

To dissect out the salivary glands, prepare the mosquito as directed above. Then make two clean cuts across the thorax as indicated in Fig. 242. The salivary glands are minute glands lying in the thorax just above and slightly in front of the first pair of legs (Fig. 242 S.). Place the cut-off anterior portion in a drop of saline solution. Insert a needle in the head and one in the thorax above the second pair of legs. Then by gently drawing the two needles apart the neck membrane should rupture and the glands and other tissues be drawn out. The salivary glands may be recognized by their glistening appearance and their structure. Patton recommends, after removing the wings and legs, placing the entire mosquito in some saline solution; then insert a needle in the head and another in the thorax; make a number of gentle pulls with more or less side to side movement; at the same time exert pressure on the thorax to force the blood into the head. This will cause the neck to bulge; if these movements are gently continued, the membrane will break and the glands may be drawn out and examined as already indicated.



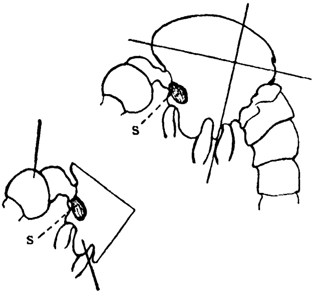


Fig. 241 (*left*). The dorsum of the abdomen of a mosquito with needles in position for cutting around the tip of the seventh abdominal segment. (2) Needles in position gradually to withdraw the intestinal tract.

Fig. 242 (*right*). The upper figure shows the two cuts across the thorax of a mosquito preparatory to the removal of the salivary glands. The lower figure shows the needles in position ready to pull out the glands. S, position of glands.

To determine the presence of the malaria sporozoites or oocysts it is not necessary to fix and stain the salivary glands or the stomach. Simply mount in saline solution and examine with the high powers of the compound microscope. The characteristic sporozoites can be seen in the glands or in the surrounding fluid; the oocysts can be recognized in the walls of the stomach. If a staining is desired, tease out the glands or stomach so that they adhere firmly to the slide but do not allow them to become dry. Fix and stain with one of the Romanowsky's stains. (Wright's modification is an excellent routine stain; it can be purchased of any reputable house dealing in chemical reagents.)

For the dissection of other insects, fresh material, patience, and skill will reward the worker with beautiful results. A little ingenuity and not too much equipment is usually the *sine qua non* of good work.

THE REARING OF INSECTS

The methods of rearing and handling insects under experimental conditions have been developed to a high state of perfection in certain groups. It would take us too far afield and occupy too much space to outline these methods here. Instead it is proposed to call the attention of the beginner as well as the advanced student to specific articles or books that outline in some detail the methods employed by specialists. In most cases the simplest and least complicated procedure will give not only the desired but oftentimes the best results. Extensive accounts of rearing technique will be found in the various references given under the different chapters of this book. These should be consulted. Only a few will be listed in the references to be given at the end of this chapter.

Here again the most pressing problem to the average worker is the rearing of mosquitoes. In practically all genera, except the genus *Anopheles,* it is possible to determine the different species from the examination of the larvae (fourth stage). With *Anopheles* it is always desirable to breed out the adults. This can be done with the simplest of equipment. Ordinary finger bowls make excellent rearing dishes (practically any kind of dishes will serve). When making larval collections for the purpose of rearing, care should be exercised to secure larvae from definite water area types. Each collection should be kept separate and a supply of the various types of water brought in for the rearing work (ordinary tap water is usually not very suitable). Always place the larvae at first in a large dish with plenty of water. When the larvae appear in the fourth stage, separate them into individual rearing dishes, a single larva to a dish. The simplest individual rearing dish is a 6- to 8-drachm vial. These vials can be placed in a large board in which holes have been bored partially through the wood. Cotton plugs or cheesecloth will serve to close the vials. In this way large numbers of larvae can be isolated without too much labor. If the larvae are young when placed in the vials, it is desirable to change the water every second day. The writer has found the best and most easily obtainable food is yeast (Fleischmann's yeast cakes)—a small particle to each vial. Be careful not to add too much.

When each larva pupates, the larval skin should be removed, carefully expanded in water on a slide, then dehydrated (the writer starts with 70 per cent alcohol[4]), and mounted in euparal. Treat the pupal skin similarly and mount on the same slide with the larval skin. (The writer uses 5-mm. cover slips so that it is easy to mount larval skin, pupal skin, and, if a male, the genitalia on the same slide.) The adult should be pinned and some system should be devised so that slide material can be connected with the pinned specimens. If mounting of the skins is not feasible, preserve them in small vials. Always be careful to label all material. If this simple procedure is followed, extensive biological data can be secured with a minimum of labor and equipment.

MYIASIS-PRODUCING FLIES: When maggots are removed from wounds, cavities, and the like, or are passed in the feces and urine or vomited, it is highly desirable to rear the adults. It is almost impossible to make specific identifications of fly larvae. If the worker has the time and facilities he can usually determine the family to which a larva belongs by an examination of the posterior spiracles and by using the key given on page 531. In the case of specific myiasis-producing flies the writer has found (following the method devised by Walker) the simplest procedure is to place the maggot on a piece of fresh beef on about two inches of moist sand in a large glass tube. Plug tightly with cotton or cover with several layers of cheesecloth held in place by a rubber band. Examine each day and replace the meat when it begins to decay. When the maggot enters the soil remove the meat and await the emergence of the fly. Always search for the empty puparium and preserve it. In the case of semispecific myiasis-producing flies this method may serve equally well but it is preferable to use decaying vegetable matter for the maggots of most of the *Muscidae*.

Medical men should always make records of cases of myiasis and, if the maggots cannot be reared, preserve them and send to specialists. The author is always glad to receive material and will identify or obtain identification by specialists (in groups with which he is not familiar).

A NEW MOUNTING MEDIUM: Recently there has been introduced a new medium for the mounting of small insects. It is especially valuable for the permanent mounting of mites, lice, fleas, mosquito larvae, mosquito genitalia, and dissected material. The writer has found the following formula most useful (Downes, Science, 95: 633, 1942).

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[4] Cellosolve is an excellent dehydrating medium. Start with a 50 per cent mixture of cellosolve and water; then go directly to pure cellosolve. Mount in euparal without further clearing.

Dissolve polyvinal alcohol (of medium vicosity) in hot water till it makes a thick syrup. This is the stock solution. Make up the medium as follows:

Stock solution	56%
Lactic acid	22%
Phenol (C.P.)	22%

The percentages are all by volume. Mix the lactic acid and phenol in a warm solution (stock) until it clears. If bubbles form, heat the mixture and allow it to stand until it is clear. Store in bottles and use as a mounting medium. Mounting can be done directly from water, with living or dead material. Cover with the usual cover slips; drying and hardening are rapid. For rapid clearing the slides may be warmed. Such mounts appear to be permanent.

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Consult the references under each of the groups treated in this book. Practically every worker gives a brief or extended account of his rearing and experimental technique.

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